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# CONTENTS

FIRST-YEAR MOVEMENTS BY JUVENILE MEXICAN SPOTTED OWLS IN THE CANYONLANDS OF UTAH. David W. Willey and Charles van Riper III .....	1
DISTRIBUTION, POPULATION SIZE AND HABITAT USE OF THE RÉUNION MARSH HARRIER, <i>CIRCUS M. MAILLARDI</i> . Vincent Bretagnolle, Thomas Ghestemme, Jean-Marc Thiollay and Carole Attié .....	8
NEST-SITE SELECTION AND REPRODUCTIVE SUCCESS OF URBAN RED-SHOULDERED HAWKS IN CENTRAL CALIFORNIA. Stephen C. Rottenborn .....	18
HABITAT USE BY RED-TAILED HAWKS WINTERING IN THE DELTA REGION OF ARKANSAS. Heath D. Garner and James C. Bednarz .....	26
AN EVALUATION OF THE ANDEAN CONDOR POPULATION IN NORTHERN ECUADOR. Marcus T. Koenen, Sarah Gale Koenen and Norma Yanez .....	33
SHORT COMMUNICATIONS	
SUMMARY OF PHILIPPINE EAGLE REPRODUCTIVE SUCCESS, 1978-98. Hector C. Miranda, Jr., Dennis I. Salvador, Jayson C. Ibañez and Gliceria A. Balaquit-Ibañez .....	37
DIET OF AUTUMN MIGRATING NORTHERN SAW-WHET OWLS ON THE EASTERN SHORE OF VIRGINIA. David M. Whalen, Bryan D. Watts and David W. Johnston .....	42
BREEDING BIOLOGY OF THE EURASIAN KESTREL IN THE STEPPES OF SOUTHWESTERN SPAIN. J.M. Avilés, J.M. Sánchez and A. Sánchez .....	45
BREEDING DENSITIES AND HABITAT ATTRIBUTES OF GOLDEN EAGLES IN SOUTHEASTERN SPAIN. Martina Carrete, José Antonio Sánchez-Zapata and José Francisco Calvo .....	48
TRAPPING ESTIMATES FOR SAKER AND PEREGRINE FALCONS USED FOR FALCONRY IN THE UNITED ARAB EMIRATES. Nigel W.H. Barton .....	53
FIRST CONFIRMED BREEDING RECORDS AND OTHER INCIDENTAL SIGHTINGS OF NORTHERN HARRIERS IN LABRADOR. Tony E. Chubbs, Bruce Mactavish, Keith Oram and Perry G. Trimper .....	56
LETTERS .....	58
COMMENTARY .....	62

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COVER: Philippine Eagle (*Pithecophaga jefferyi*). Painting by Dana Gardner.

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## FIRST-YEAR MOVEMENTS BY JUVENILE MEXICAN SPOTTED OWLS IN THE CANYONLANDS OF UTAH

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**ABSTRACT.**—We studied first-year movements of Mexican Spotted Owls (*Strix occidentalis lucida*) during natal dispersal in canyonlands of southern Utah. Thirty-one juvenile Mexican Spotted Owls were captured and radiotracked during 1992–95 to examine behavior and conduct experiments related to the onset of natal dispersal. Juvenile Spotted Owls dispersed from their nest areas during September to October each year, with 85% leaving in September. The onset of movements was sudden and juveniles dispersed in varied directions. The median distance from nest area to last observed location was 25.7 km (range = 1.7–92.3 km). Three of 26 juveniles tracked (11%) were alive after one year, although none were observed with mates. We conducted a feeding experiment, using Mongolian gerbils (*Meriones unguiculatus*), to test the influence of increased food supply on dispersal onset. The mean dispersal date of five owls that received supplemental food (Julian day no.  $255 \pm 2.6$  SD) was significantly different than a control group (day no.  $273 \pm 12.3$ ).

**KEY WORDS:** Mexican Spotted Owl; *Strix occidentalis lucida*; natal dispersal; telemetry; dispersal timing; canyonlands.

Movimientos del primer año de juveniles de *Strix occidentalis lucida* durante la dispersión en tierras del Cañon al sur de Utah

**RESUMEN.**—Estudiamos los movimientos del primer año de *Strix occidentalis lucida* durante la dispersión natal en tierras del Cañon al sur de Utah. Treinta y un buhos juveniles fueron capturados y dotados de radiotransmisores durante 1992–95 con el fin de examinar su comportamiento y conducir experimentos relacionados con la iniciación de la dispersión natal. Los buhos juveniles se dispersaron de sus áreas de anidación durante Septiembre a Octubre de cada año, con un 85% partiendo en Septiembre. La iniciación de los movimientos fué repentina y los juveniles se dispersaron en varias direcciones. La distancia media del área del nido a la última localización observada fue de 25.7 (rango = 1.7–92.3 km). Tres de los 26 juveniles monitoreados (11%) estaban vivos después de un año, aunque ninguno fue observado con compañero. Conducimos un experimento de alimentación utilizando *Meriones unguiculatus*, para probar la influencia del incremento en comida con relación a la dispersión. La fecha de dispersión media de cinco buhos que recibieron suplemento alimenticio (día no.  $255 \pm 2.6$  SD) fue significativamente diferente que el grupo de control (día no.  $273 \pm 12.3$ ).

[Traducción de César Márquez]

Study of the dispersal movements by raptors using radiotelemetry allows researchers to track in-

dividuals over prolonged time periods (e.g., Kenward et al. 1993). Using telemetry in Arizona, Ganey et al. (1998) showed that juvenile Mexican Spotted Owls (*Strix occidentalis lucida*) began dispersal each year during September, and that early movements were abrupt and in random directions

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from natal areas. In the Pacific Northwest, Spotted Owls (*S. o. caurina* and *occidentalis*) showed similar first-year movement patterns (Gutiérrez et al. 1995).

Although numerous studies of Spotted Owls have reported on early dispersal movements (Gutiérrez et al. 1995), few individuals have been observed to settle and find mates. This is likely due to the expense and difficulty of tracking birds over long distances and time periods, and due to high mortality rates. Because natal dispersal is defined as the movement of an individual from its birth site to the place where it reproduces (Howard 1960), few studies have examined true dispersal in raptors (Koenig et al. 1996). Only studies of Eastern Screech-Owls (*Otus asio*) and Burrowing Owls (*Athene cunicularia*) have used an experimental approach to assess proximate factors responsible for the onset of dispersal (Ritchison et al. 1992, Belthoff and Dufty 1998, King 1996).

In southern Utah, Mexican Spotted Owls occupy arid rocky canyon habitat within a matrix of desertscrub vegetation communities (Brown 1982, Willey 1995). Our goal was to examine aspects of Mexican Spotted Owl natal dispersal timing and preliminary movements in Utah, and attempt to track the owls using radiotelemetry from aircraft as long as possible. Our objectives were to describe first-year movement patterns by juvenile Spotted Owls and conduct field experiments to examine proximate mechanisms that influence the timing of natal dispersal by owls.

#### STUDY AREA AND METHODS

Field work was conducted at four study areas in southern Utah: Zion, Capitol Reef and Canyonlands National Parks, and on the Manti LaSal National Forest (Fig. 1). The Zion National Park study area was located 1 km north of Springdale, in southwestern Utah. Capitol Reef was located 25 km northeast of Torrey in southcentral Utah. Canyonlands National Park was located 45 km southwest of Moab, Utah and the Manti LaSal was located on Elk Ridge 35 km east of Blanding in southeastern Utah. All areas were characterized by steep sandstone canyons isolated among alluvial valleys and uplifted plateaus (Thornbury 1965). Elevations ranged from 1109–3960 m. Total annual precipitation averaged 17 cm per yr and temperatures ranged seasonally from <0–>40°C (U.S. Weather Bureau, Climate and Precipitation Summaries, Utah). Pinyon-juniper (*Pinus edulis-juniperus utahensis*) woodland and desertscrub vegetation dominated the landscape matrix (Brown 1982). Canyon vegetation included small patches of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), pinyon pine (*Pinus monticola*) and Utah juniper (*Juniperus osteosperma*). Box elder (*Acer negundo*), bigtooth

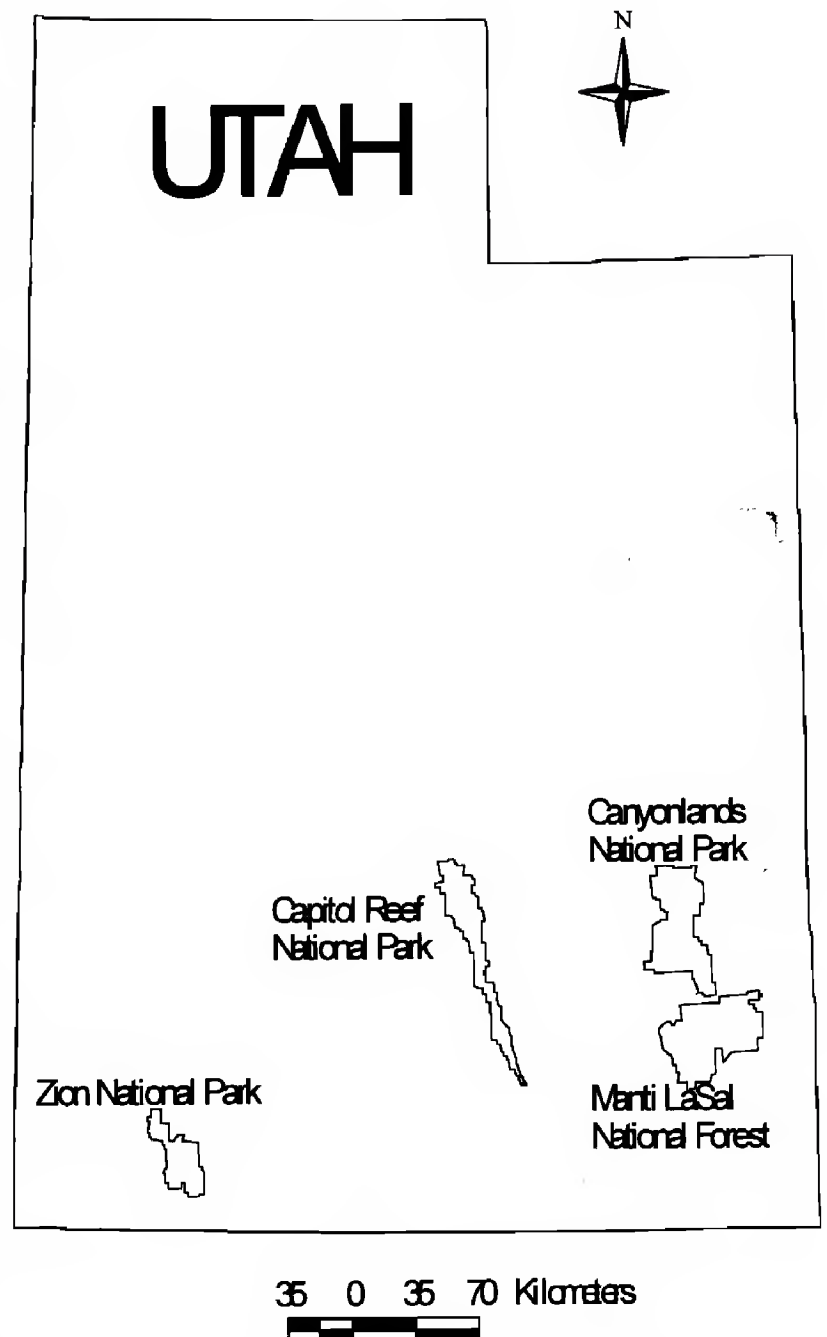


Figure 1. Location of four primary study areas where Mexican Spotted Owl natal dispersal was investigated in Utah during 1992–95.

maple (*A. grandidentatum*), Frémont cottonwood (*Populus fremontii*) and willows (*Salix* spp.) were present along mesic canyon bottoms and cliff seeps.

Juvenile Spotted Owls were trapped during 1–15 August each year of the study using Bal-Chatr traps or noose poles (Forsman 1983). Radiotransmitters (model RI-2C, Holohil Inc., Ontario, Canada), weighing 5.5–6.0 g with signal life ranging from 12–24 mo, were attached to the two central rectrices using quick-set epoxy and unwaxed dental floss (Reid et al. 1996).

We received radio signals using TR-4 and TR-2 receivers with handheld or airplane mounted H-antennas (Telonics Inc., Mesa, Arizona). Locations were based on aerial fixes or visual observation of roosting owls. We recorded the Julian date, time and Universal Trans Mercator coordinates for each owl location. From early August until the owls dispersed, we attempted to relocate owls every day. Once the owls began large movements outside of the natal area, we relocated them every 3–7 d. When owls could not be located by ground tracking, we



searched out 100 km in all directions from the last known location with fixed-wing aircraft.

We defined the beginning of Spotted Owl natal dispersal as the time when an individual initiated movement that led away from the nest site a distance equal to 1.68 km, the radius of a circle equal to an average adult home range (Willey 1998). We assigned the dispersal day to the Julian date halfway between the last known day in the natal area and the first day confirmed outside of the natal area. We assumed that dispersal movements ended when a juvenile settled on a home range and found a mate.

Total distance moved was defined as the sum of distances moved between successive relocations from the time a juvenile began dispersal to the last known location. Final distance was defined as the straight-line distance between the nest location and last known location. Movement rate (m/d) was defined as the distance between successive locations divided by the time interval. We determined azimuth from the nest site to final location for each individual and then estimated the dispersal direction and the angular dispersion around the mean direction (Batschelet 1981) for all individuals and each cohort (i.e., each year's group of juveniles). Rayleigh's test (Zar 1974) was used to determine if movements were random with respect to direction for individuals, among and within cohorts.

We conducted field experiments to examine hypotheses about proximate factors that influence the onset of natal dispersal. Our first hypothesis was that juveniles dispersed from the parental home range to search for food, an "Economic Hypothesis." The null hypothesis was that there would be no difference in the timing of dispersal between juvenile Spotted Owls that were given supplemental food and juvenile Spotted Owls that were not supplemented. An alternative hypothesis was that owls with food supplements would show a later dispersal date than owls not fed that leave to search for food outside the natal area ( $H_{a1}: v_1 > v_2$ ). If dispersal onset was controlled by body condition rather than food availability, we postulated that the additional food would cause the treatment owls to leave sooner than controls ( $H_{a2}: v_1 < v_2$ ).

An alternate mechanism was that juveniles were driven from the parental home range by adults (Howard 1960). Therefore, a second null hypothesis was that there is no difference in adult aggressive behavior in the vicinity of juveniles during the week preceding and the week following dispersal. We assumed that if adults drove young from the area, then the number of aggressive calls by adults would be greater in pre- versus post-dispersal observation periods ( $H_a: v_1 > v_2$ ).

For the experiments, we located 10 juvenile Spotted Owls in August 1994 and attached radiotransmitters to their tail feathers. We were not able to determine the sex of the juvenile owls in the field; however, the age (Forsman 1983, Moen et al. 1991) and initial condition (sternal palpation) of the 10 juveniles were estimated at the time of capture and determined to be quite similar among the owlets. Therefore, five owls were randomly selected for the treatment group and five for the control group. The random allocation of owls to experimental groups resulted in two sibling pairs selected for the fed group. The treatment diet was two Mongolian gerbils per d (*Meriones unguiculatus*, 350–500 g/d) fed to each

treatment owl starting on 20 August at the start of the predispersal period. Juveniles were fed two gerbils each day (one each morning and evening). Juveniles were re-located each day and fed at the location where they were found by placing the gerbils on the ground within 5 m of the juveniles. The owls were fed each day until dispersal began and we conducted direct observation to confirm each feeding. Members of the control group had no food supplement. We used a two-sample *t*-test to compare the mean dispersal dates between treatment and control groups (Wilkinson 1990). Because the potential correlation in dispersal timing by siblings could bias our results, we repeated our analysis using only independent owls in the control group (i.e., we selected the juvenile that left first in two sibling pairs). Significance for the tests was set at  $\alpha = 0.10$  (Steidl et al. 1997).

In testing Howard's (1960) "social hypothesis," we considered calls an index to adult agonistic behavior. Based on our interpretation of vocalization studies by Forsman et al. (1984) and Ganey (1990), we classified following "agitation" calls as agonistic: the bark call, screeches and sharp whistles and the agitated series call. These calls are only produced by subadults and adults, and not by juveniles. For the field test, the treatment group remained the same as the previous experiment. We selected this group because they were relatively more accessible in the rugged terrain; however, selection of this group may have biased our results because we did not know the influence of supplemental feeding on adult calls (i.e., we did not monitor calls of adults where juveniles were not fed gerbils).

We assumed that if adults chased juveniles from their natal areas we would observe aggressive vocalizations during crepuscular and nocturnal time periods when vocalizations appeared to be most common (Ganey 1990). Therefore, from mid-August–mid-September, when juveniles typically began dispersal, observers were positioned within 100 m of the juveniles and recorded calls of adults during 2-hr observation periods spaced throughout the night beginning 30 min before sunset and ending 30 min after sunrise. We sampled evenly across the night in both pre- and post-dispersal periods to account for nighttime variation in call rates (Ganey 1990). We contrasted the number of agonistic calls per hr by adults recorded each night during 1 wk pre-dispersal–1 wk post-dispersal. We tested the null hypothesis using a one-tailed paired *t*-test. Significance for this test was set at  $\alpha = 0.10$ .

## RESULTS

Thirty-one juveniles were captured and radio-tracked during 1992–95 in southern Utah (Table 1). Juveniles remained relatively close to their hatching sites until the onset of dispersal (range of locations from nest site = 67–520 m). Five owlets died prior to dispersal and were removed from the sample, leaving 26 that successfully dispersed from their natal areas. Mortality after initial dispersal was high for the 26 juveniles and only three (11.5%) were alive after 1 yr. The three owls that survived their first year appeared to settle in specific loca-

Table 1. Dispersal date, distance (km) and fate of radio-tagged juvenile Mexican Spotted Owls. Owls with no dispersal date, or distance, died in the vicinity of the nest.

OWL CODE	DISPERSAL DATE	LAST LIVE LOCATION	FATE <sup>a</sup>	FINAL DISTANCE <sup>b</sup>	TOTAL DISTANCE <sup>c</sup>
Ech474	1 Sep 92	15 Apr 93	Predation	21.2	189.9
Tw1873	5 Oct 92	5 Feb 93	Predation	10.6	39.7
Cam784	19 Sep 92	21 Nov 93	Signal lost	26.5	187.8
Cam824	15 Sep 92	6 Feb 93	Exposure	43.6	97.1
Pea514		29 May 93	Exposure		
Ele915	26 Sep 92	24 Aug 93	Signal lost	8.01	112.1
Ele574	5 Sep 92	29 Jun 93	Signal lost	1.68	136.6
Tw1374	20 Sep 93	3 Mar 94	Exposure	15.1	40.9
Tw1354		21 Nov 93	Exposure		
Spr034	11 Sep 93	4 Mar 94	Exposure	21.2	27.9
Spr123		15 Sep 93	Exposure		
Ech414	11 Sep 93	3 Mar 94	Predation	28.8	58.0
Ech683	11 Sep 93	15 Dec 93	Exposure	24.3	25.3
Ham623	10 Sep 93	8 Nov 93	Predation	47.3	54.9
Ham262	10 Sep 93	6 Feb 94	Predation	90.0	106.1
Pea175	10 Sep 93	6 Nov 93	Exposure	36.6	68.6
Bcd824	11 Sep 94	3 Nov 94	Radio molt	26.8	52.0
Bcd873	15 Sep 94	15 Nov 94	Exposure	24.8	32.2
Cam944	14 Sep 94	25 Feb 95	Predation	43.0	92.1
Fiv803	21 Sep 94	3 Nov 94	Predation	5.1	12.1
Usp983		14 Oct 94	Predation		
Dar903	21 Sep 94	1 Oct 94	Signal lost	27.7	53.3
Bsp924	15 Oct 94	21 Oct 94	Radio molt	8.9	20.2
Sco783	14 Sep 94	5 Oct 94	Signal lost	17.1	31.3
Sco854	8 Sep 94	1 Oct 94	Signal lost	51.1	58.7
Fir054	17 Sep 94	5 Oct 94	Signal lost	31.5	40.3
Usp473	12 Sep 95	11 Oct 95	Signal lost	20.1	28.0
Usp564	5 Oct 95	15 Feb 96	Exposure	92.3	110.6
Fiv034	17 Sep 95	15 Nov 95	Predation	6.0	8.3
Bur354		10 Dec 95	Exposure		
Tex262	24 Sep 95	27 Oct 95	Signal lost	30.8	85.0

<sup>a</sup> Fate indicated the outcome of tracking; signal loss occurred when owl transmitters could not be relocated after extensive search, radio molt refers to owls that dropped transmitters due to feather molt; exposure refers to owls that apparently starved to death, predation refers to owls that appeared to have been killed by predators, although scavenging may have occurred.  
<sup>b</sup> Final distance was estimated as the straight-line distance from the nest to the last observed location of an owl.  
<sup>c</sup> Total distance was estimated as the sum of the distance between all successive locations observed during dispersal.

tions and their radio signals stopped transmitting during the following summer. None of the juveniles that survived were found with mates, despite extensive surveys, before their signals terminated.

The final distance dispersed by owlets averaged  $29.2 \pm 22.48$  km ( $\pm$ SD) but varied substantially (range = 1.68–92.3 km). Movement rate of individuals also varied, with periods of no movement followed by periods of rapid movement in a few days (Table 2). Four individuals averaged >7 km/d during brief periods. The total distances traveled by owls was positively correlated with number of

relocations/owl (Spearman's rank correlation,  $r = 0.723$ ). Final distance traveled was not correlated with the number of months the owls were tracked ( $r = -0.093$ ).

The mean dispersal direction (Batschelet 1981) of all owls varied greatly and no significant directional pattern was determined within any cohort (Rayleigh's test,  $P = 0.687, 0.462, 0.104$  and  $0.371$ , 1992–95, respectively). Rayleigh's test was significant ( $P < 0.05$ ) for five individual owls and suggested that these owls exhibited directional, versus random, movement during the portion of the dis-



Table 2. Moment rates (m/d) estimated for 20 radio-tagged Mexican Spotted Owls with  $N \geq 4$ , where  $N$  = number of relocations during the dispersal period.

CODE	YEAR	N	MEAN	SE	MIN (m/d)	MAX (m/d)
Ech474	1992	29	902	290	11	7476
Twis73	1992	27	301	88	12	2095
Cam784	1992	52	910	206	5	7530
Cam824	1992	15	709	180	2	2632
Ele915	1992	53	464	77	0	3641
Ele574	1992	46	619	171	0	7738
Twis374	1993	9	195	76	2	765
Spr034	1993	8	286	76	27	698
Ech414	1993	7	583	244	11	2057
Ech683	1993	4	718	320	22	1589
Ham623	1993	9	277	179	8	424
Ham262	1993	11	500	271	0	3192
Pea175	1993	15	1382	504	0	6787
Bcd824	1994	6	3209	1463	185	9367
Cam944	1994	5	6692	2073	771	2232
Fiv803	1994	5	569	384	2	2273
Soc783	1994	11	631	117	258	1451
Sco854	1994	4	3698	860	338	6038
Tex262	1995	11	1189	279	57	2844
Usp564	1995	7	738	333	48	271

persal period that we monitored. The directional movement of the remaining juveniles was apparently random and most owls appeared to wander the landscape, switching direction frequently. Three juveniles that survived for at least 1 yr eventually reversed their direction of travel back toward the natal area and two (Ele915 and Ele574, Table 1) were last observed within 8.01 and 1.68 km of their nest sites when radio signals were lost.

We observed movements by five sibling pairs in southern Utah. Dispersal date of siblings was positively correlated ( $r = 0.73$ ) and suggested that siblings begin dispersal at similar times. When we calculated the azimuth between the nest site and final location, siblings showed a tendency to disperse at least  $100^\circ$  apart, suggesting they selected different travel paths during dispersal. The angle between sibling paths was even greater when the estimate "mean direction of travel" (Batschelet 1981) was used for this comparison (i.e., sibling paths were  $180$ – $209^\circ$  apart).

We estimated to within 1 d when individual owls dispersed from their natal area for 26 individuals during the study (Table 1). During 1992–95, dispersal began during a 6-wk period from 1 Septem-

ber–15 October. Eighty-five percent of the juveniles dispersed during September and 15% in October. The mean day of dispersal did not differ among the four cohorts (ANOVA,  $P = 0.063$ ,  $F = 2.68$ ,  $df = 35$ ), with 1992–95 cohorts dispersing during 1 September–5 October, 10–20 September, 8 September–15 October and 12 September–5 October, respectively. The overall mean day of dispersal was 17 September ( $\pm 9.8$  d) for all owls tracked.

During the field experiments, owls given supplemental food dispersed significantly earlier ( $\bar{x} = 12$  September  $\pm 2.6$  d) than the control owls ( $\bar{x} = 30$  September  $\pm 12.3$  d) as predicted by our second alternative hypothesis (two-sample  $t$ -test,  $t = -2.75$ ,  $df = 8$ ,  $P = 0.025$ ). When we repeated the test with independent observations (i.e., we eliminated 2 siblings), the difference in mean dispersal date remained significant (two-sample  $t$ -test,  $t = -2.92$ ,  $df = 5$ ,  $P = 0.033$ ). For the social hypothesis, we failed to reject the null hypothesis of no difference (paired  $t$ -test,  $t = -0.954$ ,  $df = 4$ ,  $P = 0.44$ ) in the number of agonistic calls by adults during the pre-dispersal period (192 hr of observation during 21 nights) and the post-dispersal period (202 hr of observation during 21 nights). On average, 0.66 ( $\pm 1.63$ ) agonistic calls/hr were recorded during pre-dispersal and 0.97 ( $\pm 1.74$ ) calls/hr during post-dispersal in the vicinity of three adult pairs. Retrospective power analysis indicated that the power of the test to reject the null hypothesis did not exceed 0.20. Therefore, these results are inconclusive with respect to adult behavior toward juveniles prior to dispersal.

#### DISCUSSION

Factors that influence the onset of natal dispersal include endogenous mechanisms, where control is governed by genetically-based systems, and exogenous mechanisms, in which timing is a response to local factors, including food availability, body condition and social interactions (Ferrer 1993). During our study of Mexican Spotted Owls, we observed a narrow window for the onset of dispersal among four cohorts (similar to other studies, e.g., Gutiérrez et al. 1985, 1995, Ganey et al. 1998). This provided strong evidence that ontogenetic processes control the season when Spotted Owls begin dispersal.

On the other hand, the results of our feeding experiment, which showed a significantly earlier departure period for food-supplemented owls, implied that physical condition may supply the prox-



imate signal for owls to leave the natal area. Belthoff and Dufty (1998) reported that dominant screech-owls dispersed earlier than subordinates and, based on body size and mass evidence, they assumed that dominant owlets were in better physical condition than the subordinates. Ellsworth and Belthoff (1999) showed that dominant juvenile screech-owls dispersed first (in five of seven broods) and they concluded that dominance influenced the timing of dispersal but not the distances traveled to overwinter sites. Therefore, among some owls, variation in timing of natal dispersal may also be related to competitive ability.

Juvenile owls that leave the natal area in good condition may avoid use of critical muscle protein and may be more likely to survive during dispersal. Nilsson (1989) suggested that juveniles that dispersed relatively early may also have a better chance to settle in suitable habitat. Selection could favor individuals that disperse as soon as they are fit if vacant territories are limited; however, field studies of Spotted Owls do not support a relationship between dispersal date and age at first breeding (Gutiérrez et al. 1995). Furthermore, Spotted Owls do not establish territories until at least 1-yr old and few survive their first year.

Primarily due to low power and bias due to unknown effects of supplemental feeding, the result of our "Social Hypothesis" experiment was inconclusive with respect to whether juveniles were forced out of natal areas by adults. In a study using radiotelemetry to examine adult home ranges, Willey (1998) showed that during August–September adults typically moved out of natal areas to other portions of their home ranges and were far from juveniles during the onset of dispersal. Northern Spotted Owl adults also stop feeding juveniles in mid- to late August and show no evidence of aggression toward young before dispersal (E.D. Forsman pers. comm.). Thus, we believe that social interactions between adults and juveniles were not responsible for the onset of dispersal.

Results from our analysis of dispersal behavior were similar to Spotted Owls reported from a variety of landscapes. For example, Ganey et al. (1998) reported a median dispersal distance of 16.9 km (range = 0.6–72.1 km) for juveniles tracked in mixed-conifer forests versus our median of 25.7 km (range = 1.68–92.3 km) in Utah. Ganey et al. (1998) observed that Mexican Spotted Owls initiated dispersal abruptly during September and October and showed no obvious directional pat-

terns. We observed similar patterns for four cohorts in the canyonlands of Utah.

In Arizona, New Mexico and Utah, Mexican Spotted Owls were observed moving across open low desert landscapes between islands of suitable breeding habitat (Ganey et al. 1998, Stacey pers. comm., Willey 1998). Gutiérrez et al. (1996) observed movement of Mexican Spotted Owls between "Sky Island" mountain ranges in New Mexico. Observation of long-distance movement by dispersing juveniles provides evidence that widely spaced enclaves have potential connectivity and isolated populations may have genetic significance to the owl's conservation (Keitt et al. 1995, Gutiérrez and Harrison 1996, Seamans et al. 1999).

In Utah and elsewhere across their range, predation and death caused by exposure (e.g., starvation, dehydration and disease) appeared to be the primary causes of juvenile mortality during dispersal (Gutiérrez et al. 1985, Ganey et al. 1998, Miller et al. 1997, Willey 1998). In Utah, only three owls survived their first year (90% mortality) and we found it interesting that two of the three settled relatively close (1.7–8.0 km) to their natal areas. We also observed juveniles that died while moving back toward natal areas in early spring. Therefore, studies that do not follow juveniles to the place of first reproduction (i.e., recruitment into the population) may bias their estimates of mean and median dispersal distances. This bias could be non-trivial with regard to population modeling. In addition, knowledge of each individual's sex is important because dispersal may be sex-biased. In the Pacific Northwest, female Northern Spotted Owls have been observed traveling much further than males (E.D. Forsman pers. comm.). Therefore, we strongly urge that future studies of owl dispersal collect blood samples to determine sex of each juvenile.

#### ACKNOWLEDGMENTS

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## DISTRIBUTION, POPULATION SIZE AND HABITAT USE OF THE RÉUNION MARSH HARRIER, *CIRCUS M. MAILLARDI*

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**ABSTRACT.**—On Réunion Island, Indian Ocean, the only surviving resident raptor is the endemic Réunion Marsh Harrier, *Circus m. maillardi*. It has been considered conspecific with the Madagascar Marsh Harrier (*C. m. macroscyles*) but a reanalysis of the classification of both is needed. A survey was carried out on the island in 1997–98 and the breeding population was found to be no larger than 100 pairs, mostly concentrated in forested areas at mid-elevations (300–700 m) and down to sea level, but rarely above 1200 m. The distribution of pairs was clumped with as many as 8 pairs within a 10 km<sup>2</sup> patch, and mostly concentrated in low degraded native woodlands on steep slopes. Foraging habitats were more diversified and were widely distributed from coastal wetlands to cultivated fields, forest and upper montane vegetation. Breeding was apparently not synchronized among pairs but egg laying occurred primarily from December–March. The Réunion Marsh Harrier must be considered as Threatened, although its distribution has apparently not declined between 1976–98.

**KEY WORDS:** Réunion Marsh Harrier, *Circus m. maillardi*; Indian Ocean; population size, habitat use.

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Distribución, tamaño de población y uso de habitat de *Circus m. maillardi*

**RESUMEN.**—En las Islas Reunión, Océano Indico, la única ave rapaz residente es *Circus m. maillardi*, la cual ha sido considerada como *C. m. macroscyles*, al respecto, una revisión de la clasificación de estas dos es requerida. La investigación realizada en la isla entre 1997–98 encontró que la población reproductiva no era mayor de 100 pares, concentrados en áreas boscosas en elevaciones medias (300–700 m) descendiendo hasta el nivel del mar, raras veces sobre los 1200 m. La distribución de las parejas fue aglomerada, se encontraron hasta 8 parejas dentro de un parche de 10 km<sup>2</sup>, casi siempre concentradas en áreas de bosque nativo degradadas en pendientes inclinadas. Los hábitos de forrajeo fueron mas diversos, ampliamente distribuidos desde los humedales costeros hasta áreas cultivadas, bosques y vegetación montana de altura. La reproducción no fue sincronizada entre parejas, esta ocurrió desde Diciembre a Marzo. *C. m. macroscyles* debe ser considerado como amenazado, aunque su distribución aparentemente no ha declinado entre 1976–98.

[Traducción de César Márquez]

Within the group of large harriers (i.e., the Marsh Harrier *aeruginosus* complex, *sensu* Sibley and Monroe 1990), detailed information on their ecology is only available for *aeruginosus* in Europe (review in Clarke 1995), *approximans* in Australasia (review in Marchant and Higgins 1993) and to a lesser extent for *ranivorus* in Africa (see Simmons

1997). The biology of the Réunion Harrier is very poorly known, except for its morphology and molt (Nieboer 1973) and some aspects of its breeding biology (Clouet 1978).

Réunion Island (2515 km<sup>2</sup>, maximum 50 × 70 km) is larger, more forested and has a lower human population density than the other two Mas-

carene Islands (Mauritius and Rodrigues) in the Western Indian Ocean. Both Mauritius and Réunion Islands have only one raptor still surviving, a kestrel and a harrier, respectively (Sinclair and Langrand 1998). The Madagascar Marsh Harrier (*Circus maillardi*), hereafter called the Réunion Harrier, is now the only raptor breeding on Réunion. There is some controversy with regard to its taxonomic status and it is currently divided into two well-marked subspecies, *C. m. maillardi* (Réunion) and *C. m. macrosceles* (Madagascar and Comoros) (Howard and Moore 1980), but the Réunion population may well deserve full specific status. The population size of the Réunion Harrier on Réunion was previously estimated at 200–300 pairs (Clouet 1978, Barré et al. 1996), but no standardized surveys were used to obtain these estimates. In earlier times, the species was considered to be abundant (Dubois 1672, in Barré et al. 1996), although no measure of abundance or relative abundance was provided.

We undertook a survey to assess the current status, population size and trends of the Réunion Harrier and to identify its conservation needs. This paper provides the first comprehensive account of the harrier on Réunion. Based on censuses carried out in 1997–98, we provide a provisional distribution map and a current population estimate for the whole island. We also summarize available data on the habitat use and breeding period, based on unpublished information gathered between 1987–98.

#### STUDY AREA

Réunion Island (21°15'S, 55°30'E) is a volcanic island, 2–3 million years old. It is 165 km from Mauritius, the nearest island, and 700 km east of Madagascar (Fig. 1). Most of the island is mountainous and steep. Three large and deep cirques (caldeiras), Mafate, Cilaos and Salazie, surround the highest peak (Piton des Neiges, 3069 m). An active volcano (Piton de la Fournaise, 2631 m) in the southeast is the second highest summit. Coastal lowlands are now totally cultivated or urbanized. Below 1300 m, degraded native forest is restricted to the steepest slopes. The mean annual rainfall is highest on the eastern (windward) side of the island, increasing from 3 m on the coast to 8–12 m between 1300–1900 m elevation and decreasing above 2000 m elevation (Barcelo 1996). Precipitation declines markedly on the eastern (leeward) side, down to 1 m on the southwestern coast. The mean annual temperature decreases from 24–26°C in the lowlands to 12°C around 2000 m elevation where frost is frequent in winter (June–August). Major cyclones occur every 5–10 years during the hot rainy season (December–April), but tropical storms with heavy rainfalls are of almost yearly occurrence.

The island was discovered in the 16th century and was

heavily deforested with human population growth. Massive extinctions, including 22 bird species, occurred from the early stages of colonization due to hunting pressure, introduced mammals (rats, cats, goats and pigs) and habitat destruction (Barré et al. 1996). Intensive agriculture, sprawling urbanization and construction of a dense road network are still affecting the remaining natural habitats. The native flora comprises 750 species, but 1100 additional taxa have been introduced, some of which are invading natural forest remnants (MacDonald et al. 1991). At most 55 000 ha of forest remain (Cadet 1980, Doumenge and Renard 1989, Dupont 1990) on 22% of the island area and consist of almost none of the former western dry woodlands, <1% of the original lowland mixed forest, 60% of the montane forest and 80% of the high altitude vegetation.

Five major natural habitats have been recognized (Rivals 1952, Cadet 1980, Barré et al. 1996; Fig. 1): (1) dry savanna woodland and semi-sclerophyllous forest on the coastal lowlands has almost entirely been replaced by cultivation, urbanization and introduced vegetation; (2) humid lowland mixed evergreen forest ("Bois de Couleur des Bas"), originally covered the eastern lowlands up to 800–900 m and the western side from 750–1100 m, is now largely degraded with remnants having a dense understory, dominated by an open canopy 6–15 m high; (3) upland wet mixed evergreen forest ("Bois de Couleur des Hauts"), from 800–1900 m in the east and from 1100–2000 m in the west, is richer in epiphytes and tree ferns; (4) montane forest, between 1600–2000 m, is dominated by large *Acacia heterophylla* ("Tamarins de Hauts") that are taller (15–20 m) and larger (<1.5 m dbh) than trees in mixed evergreen stands; the understory is locally rich in native bamboos (*Nastus borbonicus*), giant heath (*Philippia montana*) and stands of screw pines (*Pandanus montanus*); (5) high heath and shrubs above the tree line are 1–2 m tall and can be very dense. We also recognized the following five heavily modified habitats that are dominated by exotic vegetation; (6) monospecific exotic tree plantations of *Cryptomeria* spp., *Pinus* spp. and *Eucalyptus* spp.; (7) dry derived savannas and shrubby areas mostly in the western lowlands on abandoned fields; (8) cultivated areas, often large fields of sugarcane but sometimes with more diversified crops with tree rows, woodlots and orchards; (9) urban and suburban areas, including associated gardens, roads and tourist resorts; and (10) wetlands such as coastal ponds and marshes or lakes in the mountains that are highly restricted and modified by exotic vegetation and deforested surroundings.

#### METHODS

We conducted a comprehensive survey aimed at locating every territorial pair of Réunion Marsh Harrier. Because of the landscape heterogeneity and a perceived uneven distribution of the species, we avoided making a population estimate that relied on extrapolations from a limited number of sample areas. Instead, we surveyed most areas of natural and semi-natural vegetation and searched, as far as possible, most potentially suitable breeding habitats for harriers. This was based on our previous experiences on Réunion and the dense network of roads, forest tracks, mountain trails and viewpoints that allowed an adequate coverage of otherwise seemingly in-



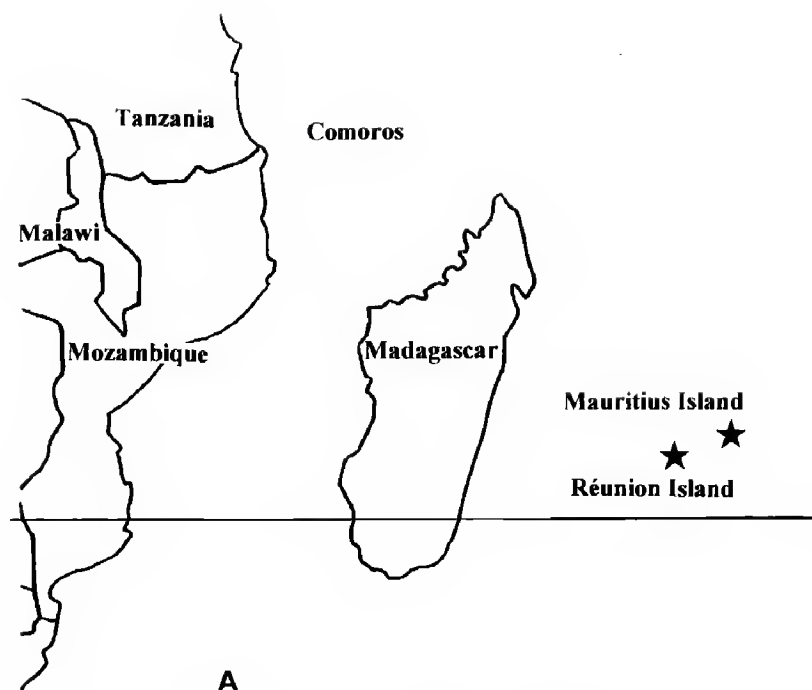


Figure 1. (A) Location of Réunion Island.

accessible areas. Observations on harriers were made during surveys from a network of 111 lookouts sampled under good weather conditions between 0700–1800 H from 23 October 1997–15 May 1998, and reported on a map using a grid of  $2 \times 2$ -km squares with each square searched for  $>1$  hr and, if possible,  $>2$  hr. Additionally, two extensive surveys (14 December and 29 March) were conducted by as many as 14 observers who simultaneously recorded the number, sex, movements and behavior of all individual harriers seen within contiguous areas from separate lookouts over a full day. The first survey method covered the most suitable areas of habitat. From each site, an area of about  $3 \text{ km}^2$  was surveyed using  $10 \times 42$  binoculars. Because of the low-flying behavior of harriers, the movements of all individuals were drawn on 1:25 000 topographical maps, using prominent landmarks. Surveys were conducted most often with two people. Therefore, we obtained an estimate of the minimum number of pairs present within a well-defined area around each lookout. In order to avoid possible double counts of the same pair on adjacent squares, we only counted those pairs whose core territory fell within the survey square.

We also used a survey method based on a grid of 577 ( $4 \text{ km}^2$ ) squares that covered the entire island. From 8 December 1997–22 January 1998, we sampled as many squares as possible. Observations were made from the most suitable viewpoint and crossed by foot or car. We considered a square to be completely surveyed if at least 60 min of continuous observation time were spent at a central point in the square, or if the total observation time for the square was  $\geq 1$  hr with periods of  $>20$  min of continuous observation in the same area. Many of these squares were sampled for  $>2$  hr. Also, during the same breeding season (September 1997–March 1998), we surveyed an additional 105 squares, some of them not previously sampled. Using such criteria, 331 ( $2 \times 2 \text{ km}$ ) squares were surveyed and the minimum number of pairs in each of them was assessed. Two pairs were considered to be different if they were seen at least once

simultaneously. Many other squares were crossed opportunistically but they were not adequately or fully surveyed because of a lack of time, inappropriate weather conditions or because they were unsuitable for breeding harriers (totally urbanized, cultivated or above treeline).

Because we focused on the identification and localization of breeding or potentially-breeding pairs, we excluded observations of individual foraging birds. The following criteria were thus used in all census methods to classify the degree of breeding evidence: a possible breeding pair was a pair of adults flying together that showed no particular breeding behavior or a single adult that performed nuptial displays; a probable breeding pair was a pair that showed territorial defense behavior, usually an adult chasing an individual of the same sex, or even talon grasping, two adults of opposite sexes that displayed together, or one in the presence of the other or adult females that gave solicitation to passing adult males; a certain or confirmed breeding pair was one with one or more young following an adult carrying a prey with persistent begging calls, an adult bringing prey or nest material to a potential nest site, prey transfer between males and females, the occupied nest was found or an empty nest was found with a pair nearby.

All observations (irrespective of sampling methodology) were plotted on a digitized map of Réunion Island using a Geographical Information System (ARCVIEW 3.b software; Environmental Systems Research Institute Inc. 1996). A grid was superimposed on the island GIS map dividing it into 577 ( $2 \times 2 \text{ km}$ ) squares whose limits crossed habitat types randomly. Among them, 85 squares overlapped the coastline and included a variable proportion of sea area. When a nest site was not precisely located and the record overlapped the limits of two squares, it was assigned to a single and most appropriate square.

Data sets obtained by the two survey methods were treated separately, but used together for estimating the distribution of population on the island. Observations from lookouts were first mapped on the island grid. We then lumped all data to produce two kinds of maps. The first summarized searching/sampling effort by giving each square a sampling status (i.e., not sampled, sampled by the first method, sampled by the second method or sampled by both methods). The second map was a general distribution map of the species. Using these maps, we determined the breeding status of harriers in each square using the highest recorded status by any of the methods.

For abundance estimates, we reported data from the two methods in each square. When harriers were observed in a given square, we summed the number of possible, probable and confirmed territorial pairs. When there were two different pairs in the same or adjacent squares, they had to have been seen simultaneously to be tallied. This meant that, if a square was surveyed using two different methods, we used the maximum number of pairs given by one method.

## RESULTS

**Surveys and Coverage of Réunion Island.** A total of 384 squares (66.6%) were adequately surveyed. Because 43 additional squares were unsuitable for

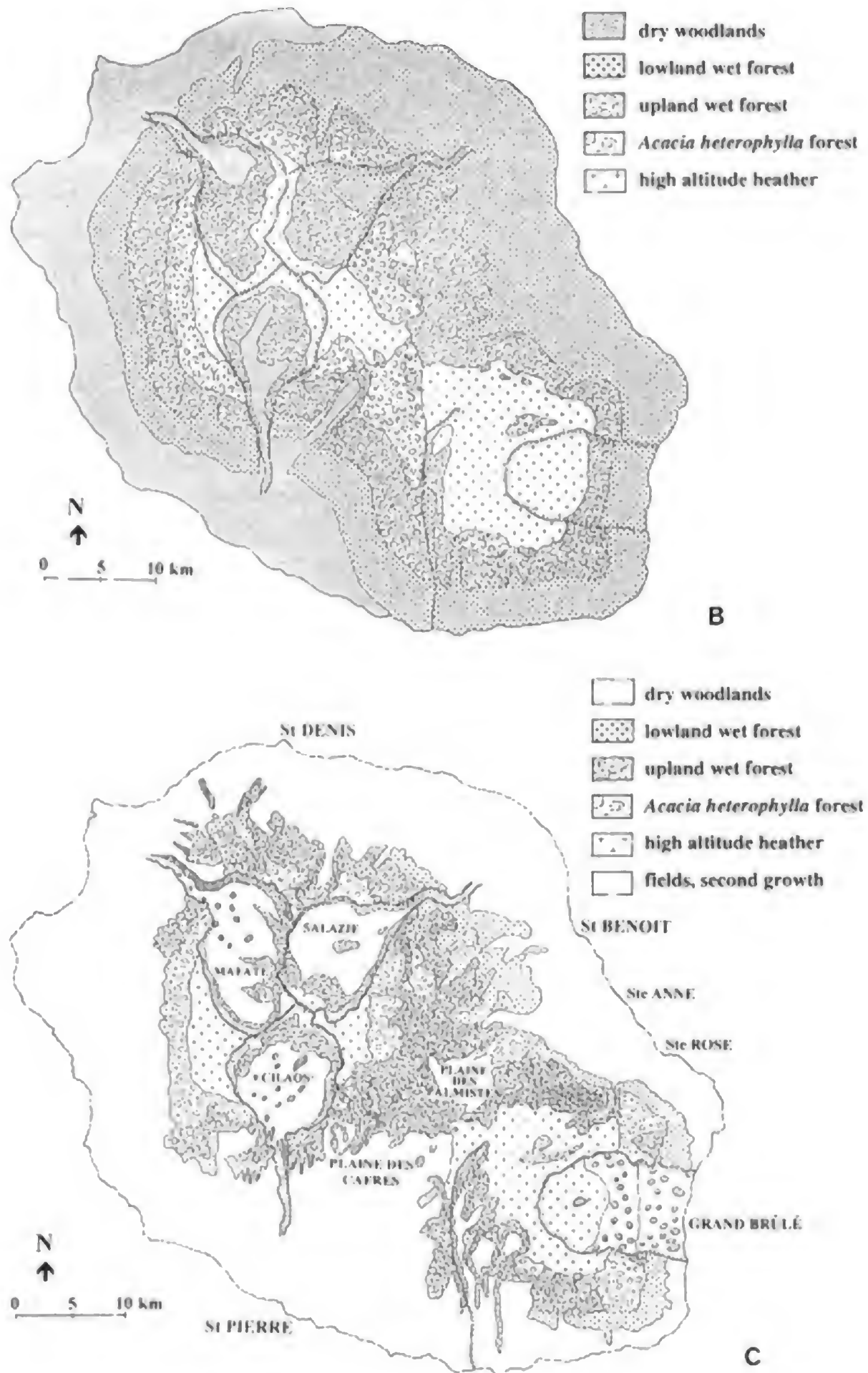


Figure 1. Continued. (B) Reconstructed distribution of natural vegetation before human colonization. (C) Current distribution of main vegetation types.

harriers, our combined survey covered 75% of Réunion Island. Surveys based on 2-hr observations from lookouts provided data on 108 squares ( $N = 111$  lookouts), while the method based on surveys

of squares resulted in 111 squares with >1 hr of observation and an additional 196 squares with a shorter census (Fig. 2). The least surveyed areas were two of the three cirques which were known



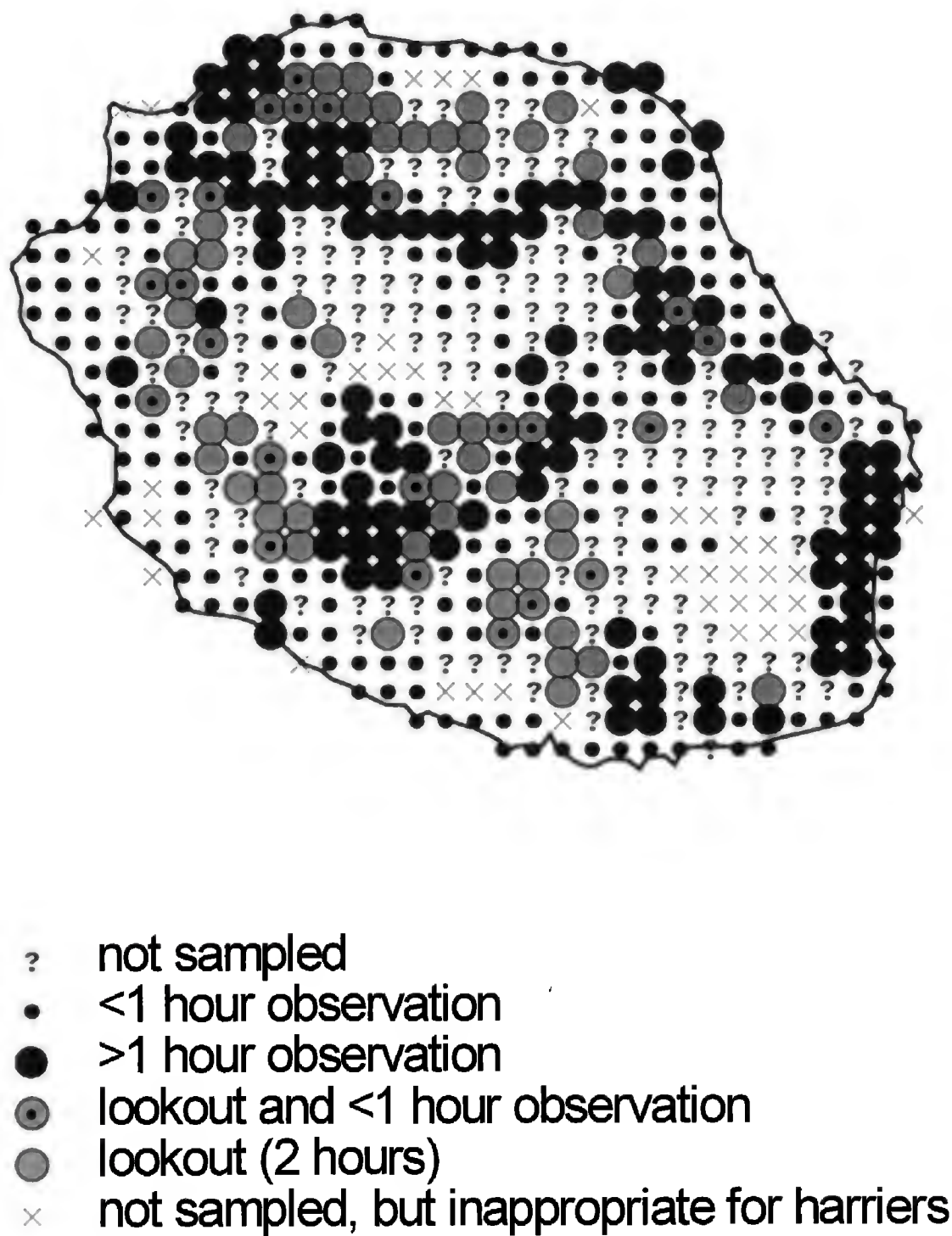


Figure 2. Harrier survey sampling sites.

to contain very few harriers and a heavily forested area in the east of the island where harriers were probably scarce due to the vegetation structure.

**Distribution Pattern of Réunion Harriers.** Overall, harriers were distributed throughout the island, with no marked preference for any region (Fig. 3). Pairs were irregularly spaced with large areas where they were absent as breeders. There were six areas where as many as 7–8 pairs were aggregated (e.g., within a 8-km segment of a valley with a density of 5–7 pairs over 16 km<sup>2</sup> [Fig. 3, see Clouet 1978 for density estimates]). Surprisingly, harriers were rare within the three large cirques with no more than 2–3 breeding pairs in each although they were abundant at the entrances of the cirques. The bottom of these cirques were rather

flat and heavily populated but their surrounding steep slopes could provide suitable breeding sites for harriers. Overall, most pairs were concentrated in the lower valleys, mostly along gullies, canyons and other steep areas, a tendency which is also apparent in some breeding seabirds.

Little or no data were available for 150 squares but many of them were unsuitable for harriers. Breeding harriers were absent from another 343 squares (60% of the island area). Possible breeders were found in 20 squares, probable breeders in 46 squares and confirmed breeders in 18 squares (Fig. 4). The rather low numbers in the latter category were due to our late searching effort during the fledging and postfledging periods (>3 mo, Clouet 1978). During this period, we observed many pairs

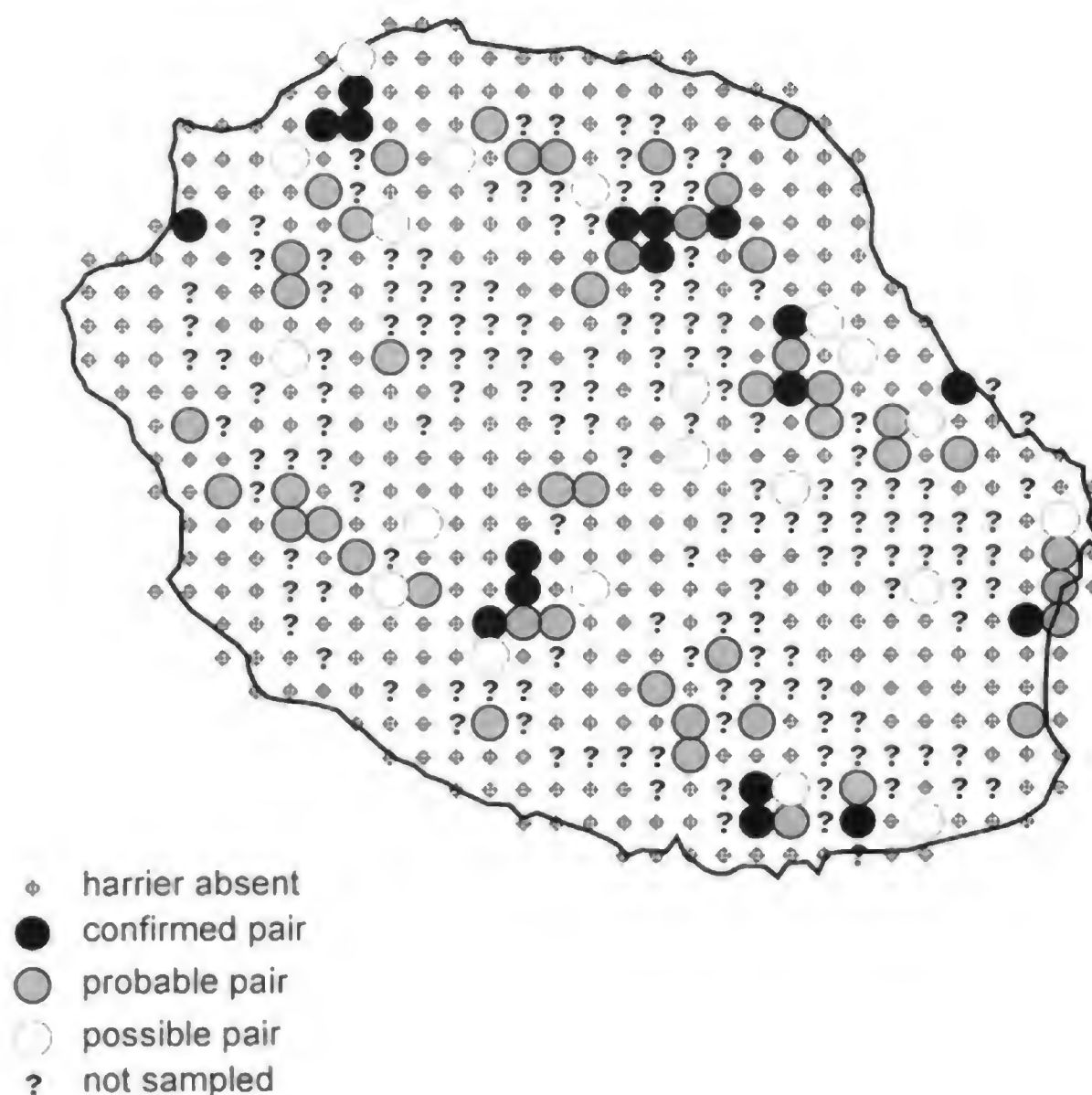


Figure 3. Harrier breeding distribution on Réunion Island according to the highest breeding status recorded per square.

feeding flying young and possibly outside their breeding territories. We treated these as probable breeders.

**Population Size.** Lumping possible, probable and certain pairs and using data from the two methods, 62 squares had a single pair, 19 squares had two pairs and 3 squares had three pairs for a total of 109 pairs. They were divided into 21 confirmed breeding pairs, 28 probable pairs, 33 family groups not belonging to any of the two former categories and 27 possible pairs (in most cases single males displaying). Nearly half of the 150 squares not adequately surveyed were in cirques or in dense natural forests and were unlikely to be used by harriers. Using the mean density estimate in squares actually sampled, we estimated that <20 pairs would have been found in the 80 unsurveyed squares. Therefore, the total estimated population could be as high as 125–130 pairs (21 confirmed, 28 probable, 33 additional families and up to 50 unconfirmed pairs). A more conservative estimate

would place the current breeding population of Réunion Harriers at about 100 pairs.

**Breeding Habitat.** Confirmed breeding pairs of harriers were distributed from 0–1200 m elevation, and up to 1800 m if probable breeding pairs and possible dispersing families were added. Overall, about 75% of pairs were below 800 m elevation and 25% were between 800–1600 m (Table 1). Most were concentrated between 300–700 m (Fig. 5), with a median altitude of 500 m ( $N = 49$ ,  $\bar{x} = 650 \pm 396$  m  $\pm$  SD). We could not test for a statistical preference for mid- to low-elevation breeding ranges because of difficulties associated with assessing the availability of areas at each elevation. However, harriers clearly avoided high altitudes (>1200 m) for breeding, but there was no evidence that they selected a particular level below this limit.

Because most habitat types had a limited altitudinal distribution, there was a strong correlation between habitat choice and elevation range (Table



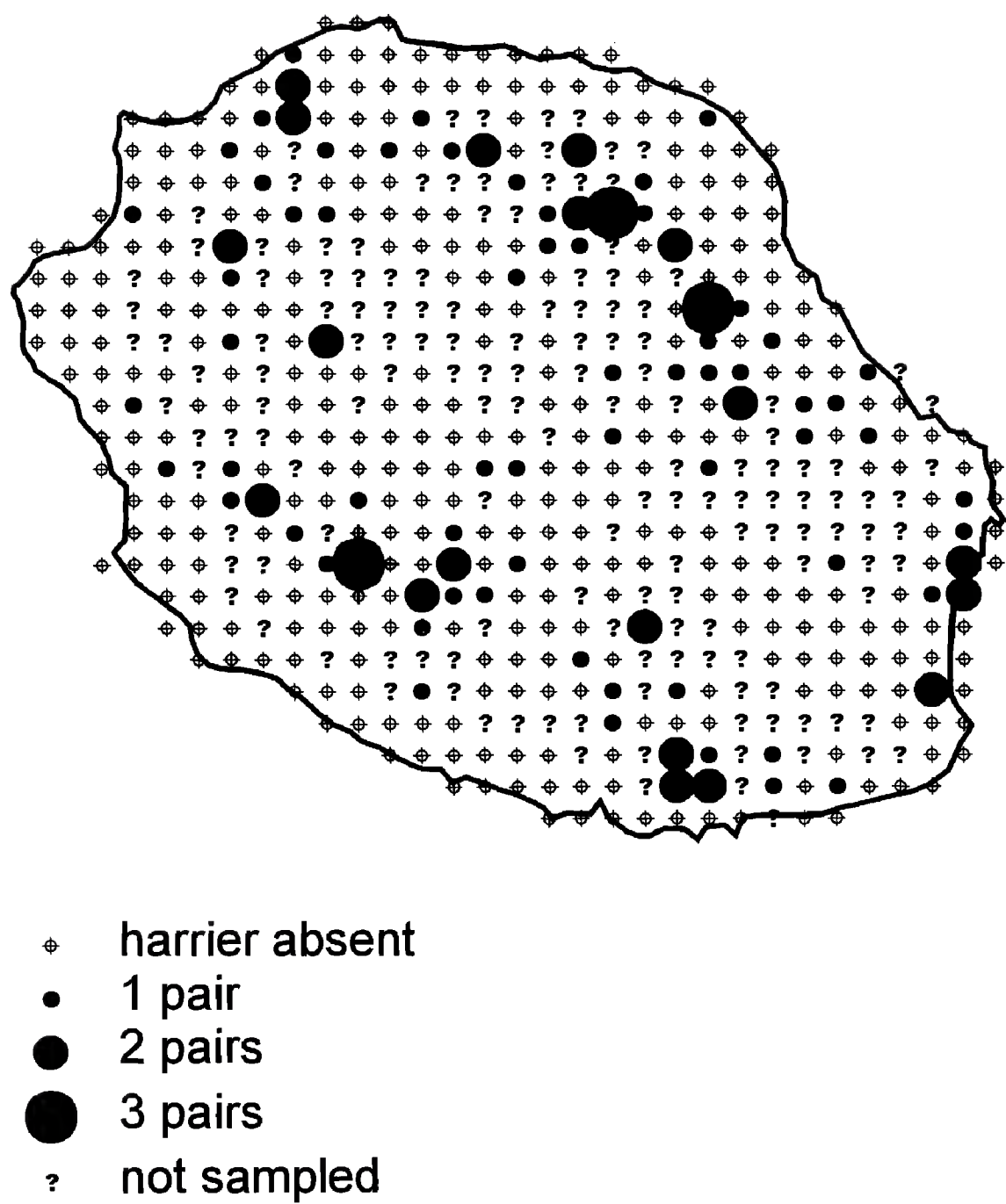


Figure 4. Harrier abundance map on Réunion Island during the 1997–98 breeding season. Number of pairs recorded per 2 × 2 km squares.

Table 1. Distribution of breeding pairs of the Réunion Harrier among habitat types.

HABITAT	HABITAT REFERENCE	ELEVATION RANGE	NUMBER OF BREEDING PAIRS	
			CONFIRMED	PROBABLE
Dry savanna woodland	1	<500	0	2
Lowland evergreen forest <sup>a</sup>	2	200–800	10	15
Upland wet evergreen forest <sup>a</sup>	3	800–1600	4	8
Montane <i>Acacia</i> forest	4	1600–2000	0	0
High altitude heathland	5	2000–3000	0	0
Exotic tree plantations	6	200–1400	0	0
Derived shrubland	7	100–600	4	2
Cultivated areas and pastures	8	0–1500	1	1
Urban and suburban areas	9	0–1300	0	0
Wetlands	10	0–600	2	0
Total			21	28

<sup>a</sup> Including secondary and degraded forests.

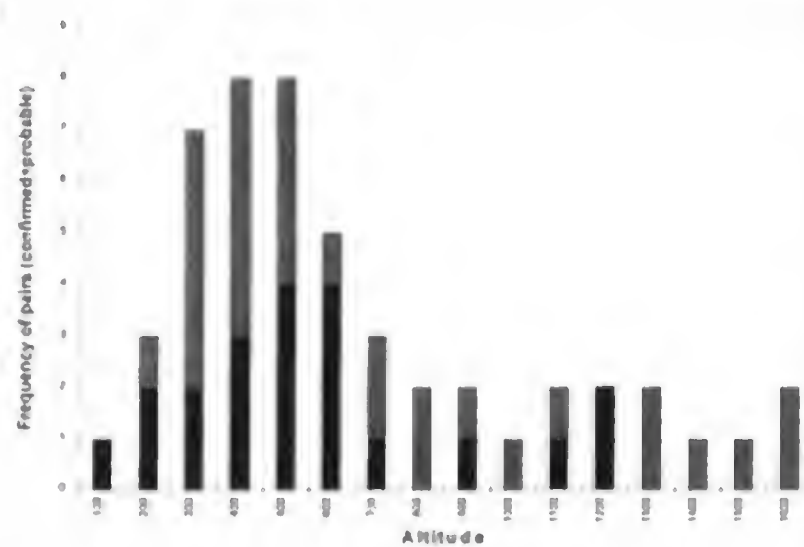


Figure 5. Altitudinal range of certain and probable pairs of Réunion Harriers during the 1997–98 breeding season.

1). Except for lowland swamp and shrubby areas, all known harrier breeding sites were in wooded areas in low, open, degraded native woodlands and were never in taller, dense forest. Nests that we found were never under a tree canopy but in open patches within forests ( $N = 6$ ), in savanna with shrubs ( $N = 12$ ) and in vegetation on cliffs or steep grassy slopes ( $N = 10$ , see Clouet 1978). No nests have ever been found or suspected to be in the widespread sugarcane fields or under primary dense forest cover.

**Foraging Habitat.** We pooled all independent observations of foraging harriers (predominantly males) obtained during census sessions ( $N = 447$ ). Foraging habitats were much less restricted than nesting habitats and included almost any habitat type, except urban and suburban areas which were apparently used in historical times (Barré et al.

1996). A minor proportion (15%) of foraging harriers were recorded over open grasslands, derived savannas, roadsides, airfields and a golf course (Table 2). The majority of them used various forested areas including low native forests, open tree plantations, shrubby clearings, heathland above tree-line and woody vegetation on steep slopes (65%). The third important foraging habitat type was sugarcane fields and pastures which accounted for 20% of the records. Few harriers foraged over dense unbroken native forests, gardens, dense mature tree plantations, coastline, stony estuaries of rivers, ponds and industrial areas (<2%). A set of randomly encountered birds, including nonforaging individuals, gave an even broader distribution. In this sample, almost any habitat was occasionally flown over, except towns and mountain slopes above 2600 m, yet low or open woodlands were still favored.

DISCUSSION

According to our observations and those of Clouet (1978), males begin to perform display flights in August–September, nest building occurs from October–November onward, egg laying from January up to April and fledglings often follow parents up to October. Our surveys (October–May) covered only part of the breeding season but, because pairs of Réunion Harriers are sedentary on their territories all year round, this survey period may have only affected the proportion of confirmed compared to possible breeding pairs and not their distribution or numbers. The time we spent in survey squares was variable from 1–>4 hr. Observation time (1 vs. >2 hr) significantly affect-

Table 2. Foraging habitat of the Réunion Harrier.

HABITAT CATEGORY	TIME SPENT (HOURS)	NUMBER OF CONTACTS	% OF CONTACTS	RECORDS PER HOUR
Dry savanna or shrubby woodlands	32	24	5.4	0.75
Wet mixed evergreen forest	31	38	8.5	1.23
Secondary native forest	91	88	19.7	0.97
Montane <i>Acacia</i> forest	11	0	0	0.00
High altitude heathland	>10	2	0.4	0.20
Exotic tree plantations <sup>a</sup>	61	199	44.5	3.26
Cultivated areas (including pastures)	57	90	20.1	1.58
Urban and suburban areas	>10	0	0	0.00
Wetlands	11	6	1.3	0.55
Total	>314	447	100	

<sup>a</sup> Including heavily degraded forests.



ed the probability of detecting the presence of harriers in a given square ( $\chi^2 = 81.7$ ,  $df = 1$ ,  $P < 0.001$ ), but there was no relationship between observation time and number of pairs detected on squares ( $\chi^2 = 0.5$ ,  $df = 1$ ,  $P > 0.05$ ). This suggested that observation time had little effect on our surveys. Therefore, we are confident that potential bias due to our methods is limited, and that the data provide a realistic estimate of both distribution and population size.

Overall, harriers were distributed throughout the island, with no marked concentration in any part of it. The current distribution probably reflected more the influence of human disturbance than true habitat preferences. Their preferred habitat occurred on rather steep and forested slopes, away from human settlements. Such characteristics are most often found along rivers, especially at cirque entrances. This suggested a currently significant level of human persecution, despite the harrier's fully protected status.

The total population in 1998 was estimated to consist of 400–600 individuals with <100 breeding pairs, although this was a conservative estimate. Uncertainties about the true population size resulted from the large proportion of birds in adult plumage which did not exhibit territorial or sexual behavior. A more accurate estimate of the breeding population size might be made if we had a better understanding of the social and breeding behavior of this species.

None of the previous estimates of the Réunion Harrier population were based on systematic searches. Therefore, estimates of the population ranged from 130–300 breeding pairs (Clouet 1978, Cheke 1987, Barré 1988, Barré et al. 1996). Our population estimate cannot be compared to previous ones because it was derived from the first complete and reliable survey of the island. Nevertheless, based on the map given by Cheke (1987) and an unpublished map (M. Clouet pers. comm.), neither the overall distribution of the harrier, nor the areas with highest densities have shown any detectable change between 1978–98. Based on 17th-century accounts (Dubois, in Barré et al. 1996), the Réunion Harrier was probably much more abundant than today. Habitat losses and faunal impoverishment following human colonization most likely caused its early decline although shooting probably played a significant role. There is no conclusive evidence showing that the harrier population has declined significantly during the last 25 yr,

despite higher population estimates at a time when its recently protected status was enforced very little. Human persecution still takes place but may be currently decreasing, and formerly cultivated or grazed areas are now abandoned, thus increasing areas of suitable habitat. Urbanization and road construction are still increasing but they occur mostly in lowlands and areas that have long been deforested and already out of the harrier's range.

Aggregation of nesters in a few areas may be due to a lack of territorial behavior of harriers away from the immediate vicinity of their nests. It exhibits a broad range of foraging habitats, a variety of hunting techniques and an eclectic prey choice, including birds, introduced mammals and some reptiles, amphibians and grasshoppers (Clouet 1978, Cheke 1987, pers. obs.). This wide niche breadth and adaptability are typical of most island birds when compared to their continental counterparts, including tropical raptors (Thiollay 1993, 1997). Nevertheless, prey abundance and accessibility are likely to be major determinants of hunting habitat selection.

Until the 16th century, the island was almost completely covered with forest. The relatively short rounded wings of the Réunion Harrier probably are an adaptation to hunt in rather dense vegetation and its relatively long middle toe is typical of a bird specialist, probably a necessity when terrestrial mammals were absent and medium-sized lower vertebrates were uncommon (Nieboer 1973). Today, large birds have disappeared but introduced rodents (*Rattus*, *Mus*), insectivores (*Tenrec*, *Suncus*), reptiles (*Calotes*, *Chameleo*, *Phelsuma*), toads (*Bufo*) and frogs (*Ptychadena*) are abundant (Probst 1997). Most of them are probably more difficult to find and catch in forests than were the once numerous pigeons and parrots (Barré et al. 1996). This may explain why this harrier tends to avoid closed canopy forest and to favor lower vegetation and more open woodlands in spite of its apparent morphological adaptation to forest. Nevertheless, it remains much more of a forest bird than any of the 12 other species of harriers in the world (del Hoyo et al. 1994).

The population of Réunion Harriers is precariously small by genetic, demographic and conservation standards. It is currently the smallest population of any native and nonmarine bird species on Réunion. It is also one of the rarest raptor species in the world and its population is now even lower than that of the fast-recovering population of the

Mauritius Kestrel (*Falco punctatus*), once the most endangered raptor in the world (Collar et al. 1994, del Hoyo et al. 1994). There is good evidence to upgrade its taxonomic status to the full specific level, distinct from the Madagascar Harrier. As a taxon of its own, and according to IUCN criteria (Collar et al. 1994), it may well deserve Endangered status because of its small population size, small range and current factors threatening its long-term survival. Although the population appears to be currently stable, this does not mean that it is at full carrying capacity and/or that carrying capacity is not declining through habitat loss or disturbance and degradation. Human population growth and economic development are very high on Réunion and the species is threatened by human persecution both from shooting and loss of breeding and foraging habitats, by increased urbanization and road construction and frequent cyclones, heavy rains and wildfires during the breeding season.

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## NEST-SITE SELECTION AND REPRODUCTIVE SUCCESS OF URBAN RED-SHOULDERED HAWKS IN CENTRAL CALIFORNIA

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**ABSTRACT.**—Fledging success was determined at nests of urban Red-shouldered Hawks (*Buteo lineatus*) in California. Fourteen of 27 nests in 1994 and 38 of 58 nests in 1995 were in exotic trees, predominantly eucalyptus (*Eucalyptus* spp.). Nesting and fledging success were higher in exotic trees than in native trees in both years, owing in part to greater stability and protective cover. Most nest trees in upland areas (>100 m from water) were exotics, and even in riparian habitats, where tall native cottonwoods (*Populus fremontii*) and sycamores (*Platanus racemosa*) were available, Red-shouldered Hawks selected eucalyptus more often than expected based on their availability. Of the habitat and nest-tree variables measured at each nest, only nest-tree height and diameter were significantly associated with reproductive success, suggesting that large, sturdy trees provided the best nest sites. Red-shouldered Hawk populations in the study area have likely benefited from the planting of exotic eucalyptus and fan palms. Reproductive success was not affected by the degree of urbanization around nest sites, as many successful nests were found in heavily urbanized areas close to human activity.

**KEY WORDS:** Red-shouldered Hawk; *Buteo lineatus*; reproductive success; riparian; exotic trees; eucalyptus.

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Selección del sitio del nido y éxito reproductivo de *Buteo lineatus* urbanos en el centro de California

**RESUMEN.**—El éxito de crianza de pichones fue determinado en los nidos de *Buteo lineatus* urbanos en California. Catorce de 27 nidos en 1994 y 38 de 58 nidos en 1995 fueron en árboles exóticos, predominantemente eucalipto (*Eucalyptus* spp.). El éxito de anidación y de crianza fue mayor en árboles exóticos que en árboles nativos en ambos años, debido en parte a la mayor estabilidad y cobertura de protección. Casi todos los árboles con nidos en áreas superiores (>100 m del agua) fueron exóticos, inclusive en habitats ribereños en donde *Populus fremontii* y *Platanus racemosa* estaban disponibles, *Buteo lineatus* seleccionó a los eucaliptos con mas frecuencia que lo esperado con base en su disponibilidad. De las variables de habitat y de árboles con nido medidas para cada nido, sólo la altura del árbol y el diametro fueron significativamente asociados con el éxito reproductivo, lo cual sugiere que los árboles grandes y fuertes proveen los mejores sitios de anidación. Las poblaciones de *Buteo lineatus* en el área de estudio aparentemente se han beneficiado de la siembra de eucalipto exóticos y palmas de abanico. El éxito reproductivo no fue afectado por el grado de urbanización alrededor de los sitios de anidación, pues muchos nidos exitosos se encontraron en áreas altamente urbanizadas cerca de la actividad humana.

[Traducción de César Márquez]

Populations of Red-shouldered Hawks (*Buteo lineatus*) have declined throughout much of the species' range during this century (Henny et al. 1973, Titus et al. 1989, Bednarz et al. 1990). Most of this decline has probably resulted from the destruction and fragmentation of hardwood forests, particularly riparian woodlands, upon which Red-shouldered Hawks are largely dependent for breeding over most of their range (Cohen 1970, Henny et al. 1973, Bednarz and Dinsmore 1981). Urbanization may also have contributed to the decline of this species, as Red-shouldered Hawks in some areas

avoid nesting near roads and buildings (Bednarz and Dinsmore 1981, Bosakowski et al. 1992).

Populations of the western race *B. l. elegans*, residing primarily in California, have been affected by human activities to some degree. Breeding primarily in riparian habitats, *B. l. elegans* declined in parts of its range early this century as a result of severe degradation of California's riparian woodlands (Willetts 1912, Grinnell and Wythe 1927), which reduced these habitats to <5% of their original levels prior to European settlement of the state (Katibah 1984). After this decline, Red-shouldered

Hawk populations appeared to be fairly stable (but low) in California from about 1950 until the late 1960s (Cohen 1970, Brown 1971, Wilbur 1973).

In the past three decades, Red-shouldered Hawk populations have increased in some parts of California. Breeding Bird Survey data indicate significant statewide increases since 1966 (Sauer et al. 1997), and local increases and range expansions have been noted in a number of locations since then (Harlow and Bloom 1989, Roberson 1993, S. A. Laymon *vide* Shuford 1993). Because riparian woodlands are still greatly reduced from their historic extent, these population increases have not resulted from recovery of the hawk's native riparian habitats, and the reasons for this recent increase are not entirely clear.

Historically, California Red-shouldered Hawks bred primarily in riparian areas, nesting in tall, native riparian trees and foraging in adjacent marshes and grasslands (Willett 1912, Grinnell and Wythe 1927, Grinnell and Miller 1944). Studies conducted in the midwestern and eastern U.S. have reported that Red-shouldered Hawks are sensitive to human disturbance and that they usually nest far from developed areas (Bednarz and Dinsmore 1981, Bosakowski et al. 1992). However, recent studies in southern California have found a number of Red-shouldered Hawks nesting in exotic trees, such as eucalyptus (*Eucalyptus* spp.) and palms (*Washingtonia* spp.), often in urban and suburban areas surrounded by development (Bloom et al. 1993, Bloom and McCrary 1996). Some Red-shouldered Hawks nest where these tall, sturdy exotic trees have been planted in upland areas, sometimes far from riparian habitats (Palmer 1988).

Bloom and McCrary (1996) have suggested that planting of eucalyptus has contributed to the expansion of this species' range and populations in California by providing suitable nest trees in upland areas (including urban areas) that were previously unsuitable for breeding Red-shouldered Hawks. However, no published studies have yet determined the breeding success of Red-shouldered Hawks in native versus exotic trees or in riparian versus upland areas. This study investigated the degree to which urban Red-shouldered Hawks nest in exotic trees and/or upland areas, the breeding success of Red-shouldered Hawks nesting in native versus exotic trees and upland versus riparian areas, and relationships between breeding success and habitat and nest tree variables related to urbanization and habitat quality.

#### STUDY AREA AND METHODS

In 1994 and 1995, I located Red-shouldered Hawk nests in the northern Santa Clara Valley at the southern end of the San Francisco Bay in Santa Clara County, California. Formerly dominated by oak (*Quercus* spp.) savanna (Clarke 1952), the northern Santa Clara Valley was covered primarily by agricultural land at the turn of the 20th century but now is dominated by residential and industrial development. These residential and industrial lands are sparsely vegetated, with relatively few trees large enough to support Red-shouldered Hawk nests. However, scattered large eucalyptus (most commonly *Eucalyptus globulus*), palms and various coniferous trees provide potential nest trees within these upland areas.

Two major streams, Coyote Creek and the Guadalupe River, as well as a number of smaller streams, flow through the urban Santa Clara Valley and from the foothills of the Santa Cruz Mountains and Diablo Ranges to San Francisco Bay. The narrow riparian corridors along the portions of these streams flowing through the Santa Clara Valley are dominated by Frémont cottonwood (*Populus fremontii*) and several species of willows (*Salix lucidum*, *S. laevigata*, *S. lasiolepis* and *S. exigua*) along their lower reaches, and by oaks and western sycamore (*Platanus racemosa*) along their upper reaches. In addition, scattered tall eucalyptus provide additional potential nesting sites within these riparian areas.

I used several methods for locating Red-shouldered Hawk nests ("nest" defined as the site of an actual nesting attempt). During late winter and spring of each year, I searched for Red-shouldered Hawks and their nests in riparian habitats along most of the streams in the study area and in upland areas. Recordings of Red-shouldered Hawk vocalizations were played frequently during surveys to elicit a territorial response from any hawks that might be present. Because Red-shouldered Hawks prefer tall trees for nesting (Bednarz and Dinsmore 1982, Dijak et al. 1990), surveys in upland areas focused on areas with tall trees. Some nests were found using data from the Santa Clara County Breeding Bird Atlas project and from locations provided by members of the Santa Clara Valley Audubon Society. Surveys were more extensive in 1995 than in 1994, particularly in upland areas.

After a nest was found, I periodically monitored it with a spotting scope until the young had fledged or until the adults had abandoned the nest (after nest failure). After young were visible in nests, I visited nests every 3–4 d until the young were near fledging age, at which point visits were made every 2–3 d. The number of young fledging from nests was estimated by the number of young seen in nests within three days of fledging. Nests abandoned before they were completed and "alternate nests" not used for nesting were excluded from analyses if it was thought that they might be located within the territory of a pair whose completed nest was included in these analyses.

Data were analyzed separately for each year. The mean number of young fledged per nest and the number fledged per successful nest (i.e., a nest from which at least one young fledged) were compared between 1994 and 1995 using Mann-Whitney *U*-tests. Kruskal-Wallis tests were used to compare the mean number of young fledging from each nest and the mean number fledging from



Table 1. Tree species used for nesting by Red-shouldered Hawks in 1994. The number of nests found in each tree species, number of nests that successfully fledged young and mean number of young per nest and per successful nest are given separately for nests in riparian areas (<100 m from the nearest stream) and upland areas (>100 m from the nearest stream).

TREE SPECIES	TOTAL NESTS	SUCCESSFUL NESTS	YOUNG FLEDGED PER NEST	YOUNG FLEDGED PER SUCCESSFUL NEST
Riparian				
<i>Platanus racemosa</i>	6	4	1.5 ± 0.5	2.3 ± 0.3
<i>Populus fremontii</i>	7	4	1.3 ± 0.4	1.8 ± 0.2
<i>Washingtonia</i> spp.	2	1	1.0 ± 1.0	2.0
<i>Eucalyptus</i> spp.	6	5	1.8 ± 0.5	2.2 ± 0.4
Upland				
<i>Washingtonia</i> spp.	2	2	3.0 ± 0.0	3.0 ± 0.0
<i>Eucalyptus</i> spp.	4	4	2.8 ± 0.3	2.8 ± 0.3

each successful nest among nests in different tree species. Mann-Whitney *U*-tests were used to compare fledging success between nests in native and exotic trees and between eucalyptus nests in upland and riparian areas, and they were also used to compare fledging success between nests attended by two adults and those attended by a pair that included a subadult (second-year) bird. All Mann-Whitney *U*-tests and Kruskal-Wallis tests were two-tailed.

In each year, the number of successful nests and the mean number of young fledging from nests was determined for each tree species, or, in the case of eucalyptus, genus. Nests were also categorized by their location relative to the nearest stream, “riparian” nests being located <100 m from the nearest stream and “upland” nests being >100 m from a stream; few riparian-associated trees (e.g., cottonwoods and sycamores) are found >100 m from a stream channel within the study area.

In a previous study of riparian tree communities (Rottenborn 1997), I had measured the diameters of all trees on 68 randomly located, 35 m-radius plots along the lower reaches of Coyote Creek, Guadalupe River and Los Gatos Creek. Using these data, I determined the number of stems of native and exotic trees on each of the 68 plots that exceeded the diameter of the smallest tree used for nesting by Red-shouldered Hawks in the present study. A *G*-test was used to compare the mean proportion of the large-diameter stems comprised of exotic species to the proportion of hawk nests from Coyote Creek, Guadalupe River and Los Gatos Creek that were in exotic trees to determine whether or not hawks used native and exotic trees in proportion to their availability within this subset of the study area. For this comparison, I used all hawk nests found along these streams over both years, counting nests used in both 1994 and 1995 only once.

Habitat and nest-tree variables thought to be related to nesting success, including nest-tree height (TREEHT), nest-tree diameter at breast height (TREEDBH), nest height (NESTHT), elevation of the nest site (ELEV) and distance from the nest to the nearest body of water (DISTWAT) were measured at each nest. Within radii of 200 and 500 m of each nest, the percent cover by artificial surfaces (ARTIF200, ARTIF500), including buildings

and pavement, was estimated from aerial photos, and the distance from each nest to the nearest building (DIST-BUIL) and paved road (DISTPAVE) was measured. Differences in the mean values of these variables at successful and unsuccessful nests were tested using Mann-Whitney *U*-tests. In addition, simple linear regressions of each of these habitat variables versus the number of young fledging from each nest were conducted. These analyses were conducted separately for 1994 and 1995 nests.

RESULTS

Twenty-seven and 58 Red-shouldered Hawk nests were located in 1994 and 1995, respectively. Thirteen of the 1994 nests were used again in 1995, so these two datasets were not independent and were therefore analyzed separately. Twenty-one of the 27 nests found in 1994 (77.8%) and 46 of the 58 nests found in 1995 (79.3%) were successful in fledging at least one young. When all nests were combined for each year, the mean number of fledged young per nest was 1.8 ± 0.2 (±SD) in 1994 and 1.6 ± 0.1 in 1995 (*t* = 0.9, *P* > 0.05), while the mean number of fledged young per successful nest was 2.3 ± 0.1 in 1994 and 2.0 ± 0.1 in 1995 (*t* = 0.7, *P* > 0.05).

**Use of Upland Versus Riparian Habitats.** Six of the nests found in 1994 (22.2%) and 18 of those found in 1995 (31.0%) were in upland areas >100 m from the nearest stream (Tables 1 and 2). Nests were located ≤1.7 km from the nearest body of water. When all nests were pooled, the mean distance between nests and the nearest body of water was 143 ± 69.8 m in 1994 and 110 ± 33.0 m in 1995. The mean distance from each upland nest

Table 2. Tree species used for nesting by Red-shouldered Hawks in 1995. The number of nests found in each tree species, number of nests that successfully fledged young and mean number of young per nest and per successful nest are given separately for nests in riparian areas (<100 m from the nearest stream) and upland areas (>100 m from the nearest stream).

TREE SPECIES	TOTAL NESTS	SUCCESSFUL NESTS	YOUNG FLEDGED PER NEST	YOUNG FLEDGED PER SUCCESSFUL NEST
Riparian				
<i>Platanus racemosa</i>	14	11	1.6 ± 0.3	2.0 ± 0.2
<i>Populus fremontii</i>	4	3	1.0 ± 0.4	1.3 ± 0.3
<i>Alnus rhombifolia</i>	1	0	0.0	—
<i>Washingtonia</i> spp.	1	0	0.0	—
<i>Eucalyptus</i> spp.	20	17	1.9 ± 0.2	2.2 ± 0.1
Upland				
<i>Quercus agrifolia</i>	1	1	0.0	—
<i>Washingtonia</i> spp.	3	2	1.3 ± 0.7	2.0 ± 0.0
<i>Eucalyptus</i> spp.	14	12	1.8 ± 0.3	2.1 ± 0.2

to water was 590 ± 268 m in 1994 and 302 ± 91.7 m in 1995.

With the exception of a single nest in a coast live oak (*Quercus agrifolia*) in 1995, all upland nests were in exotic trees, predominantly eucalyptus. Nest success (i.e., the percentage of nests that fledged at least one young) differed little between eucalyptus nests in riparian and upland areas (Tables 1 and 2). The mean number of young fledged from each eucalyptus nest in riparian and upland areas was 1.8 ± 0.5 and 2.8 ± 0.3, respectively, in 1994, and 1.9 ± 0.2 and 1.8 ± 0.3 in 1995. The mean number of young fledged from each successful eucalyptus nest in riparian and upland areas was 2.2 ± 0.4 and 2.8 ± 0.3, respectively, in 1994, and 2.2 ± 0.2 and 2.1 ± 0.2 in 1995. Neither of these measures of fledging success differed significantly between riparian and upland nests in either year.

**Nest Tree Species and Use of Native Versus Exotic Trees.** Red-shouldered Hawk nests were found in four tree species in 1994 (Table 1) and six tree species in 1995 (Table 2). Native trees used for nesting were Frémont cottonwood, western sycamore, white alder (*Alnus rhombifolia*) and coast live oak, while exotics included eucalyptus and fan palms (*Washingtonia filifera* and *W. robusta*). Of the 27 nests found in 1994, 13 (48.1%) were in native trees and 14 (51.9%) were in exotics. Of the 58 nests monitored in 1995, 20 (34.5%) were in native trees and 38 (65.5%) were in exotics.

Eight of 21 nests found in riparian areas in 1994 (38.1%) and 21 of 40 riparian nests in 1995

(52.5%) were in exotics, primarily eucalyptus (Tables 1 and 2). Furthermore, the percentage of nests in exotic trees along the lower reaches of Coyote Creek, Los Gatos Creek and Guadalupe River was much higher than the percentage of large trees that were exotics. Only 18% of the trees having a diameter greater than the most slender Red-shouldered Hawk nest tree were exotics, whereas 56% of the nests detected in the same areas were in exotic trees ( $G = 11.44, P < 0.01$ ). A number of nests were found in lone eucalyptus ( $N = 3$  in 1994, 8 in 1995) or small eucalyptus groves ( $N = 3$  in 1994, 12 in 1995) surrounded by mature cottonwoods or sycamores; generally, these eucalyptus were taller than surrounding native trees. Nest success seemed somewhat lower for nests in native trees than for those in exotic trees (Tables 1 and 2) in both 1994 (61.5% in natives, 85.7% in exotics) and 1995 (75.0% in natives, 81.6% in exotics), although  $z$ -tests revealed no significant differences in these percentages ( $P > 0.05$ ).

Because neither nesting nor fledging success differed significantly between riparian and upland nests in eucalyptus and fan palms, riparian and upland nests were pooled for comparison of fledging success among the nest tree species. In both years, the mean number of fledged young per nest was highest in eucalyptus, intermediate in sycamores and fan palms and lowest in cottonwoods (Fig. 1). The mean number of young that fledged per nest differed among tree species in 1994 ( $H = 8.43, P < 0.05$ ) and in 1995 ( $H = 8.57, P < 0.05$ ), primarily due to the great differences in nest success



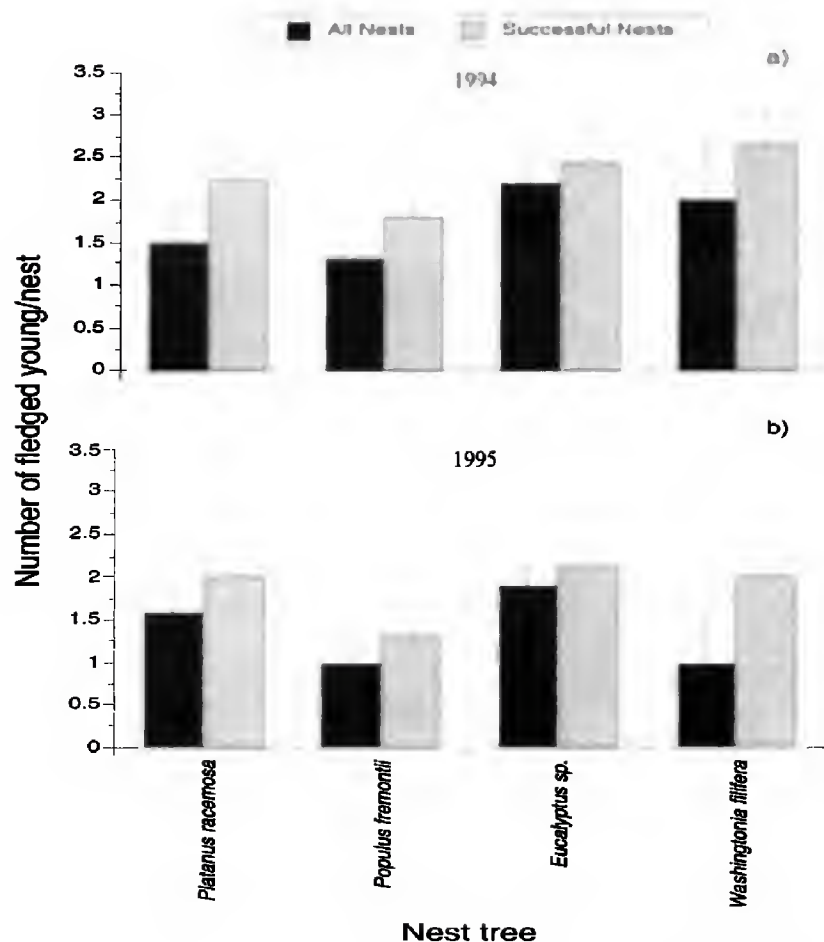


Figure 1. Mean number of fledged young per nest and per successful nest in four tree species used for nesting by Red-shouldered Hawks in 1994 (a) and 1995 (b).

between eucalyptus and cottonwood nests. Because fledging success did not differ significantly between cottonwoods and sycamores or between eucalyptus and fan palms, fledging success was pooled for all natives and compared to fledging success pooled for all exotics. The mean number of fledged young per nest was higher in nests in exotic trees than in nests in native trees in 1994 ( $U = 132$ ,  $P < 0.05$ ), although the difference was not significant in 1995 ( $t = 1.61$ ,  $P > 0.05$ ; Fig. 2).

The mean number of fledged young per successful nest did not differ significantly among tree species (Fig. 1). However, the mean number of fledged young per successful nest was significantly higher in nests in exotic trees than in nests in native trees in 1994 ( $U = 78$ ,  $P < 0.05$ ; Fig. 2). Therefore, even though the lower nest success in native trees (due to nest failures) was not a factor in these comparisons, fledging success was still found to be higher in nests in exotic trees in 1994. There was no significant difference in 1995 ( $t = 1.45$ ,  $P > 0.05$ ; Fig. 2).

In 1994, one of the 14 nests in exotics (7.1%) and five of the 13 nests in natives (38.5%) were attended by a subadult (second year) individual paired to an adult. Three of the four unsuccessful

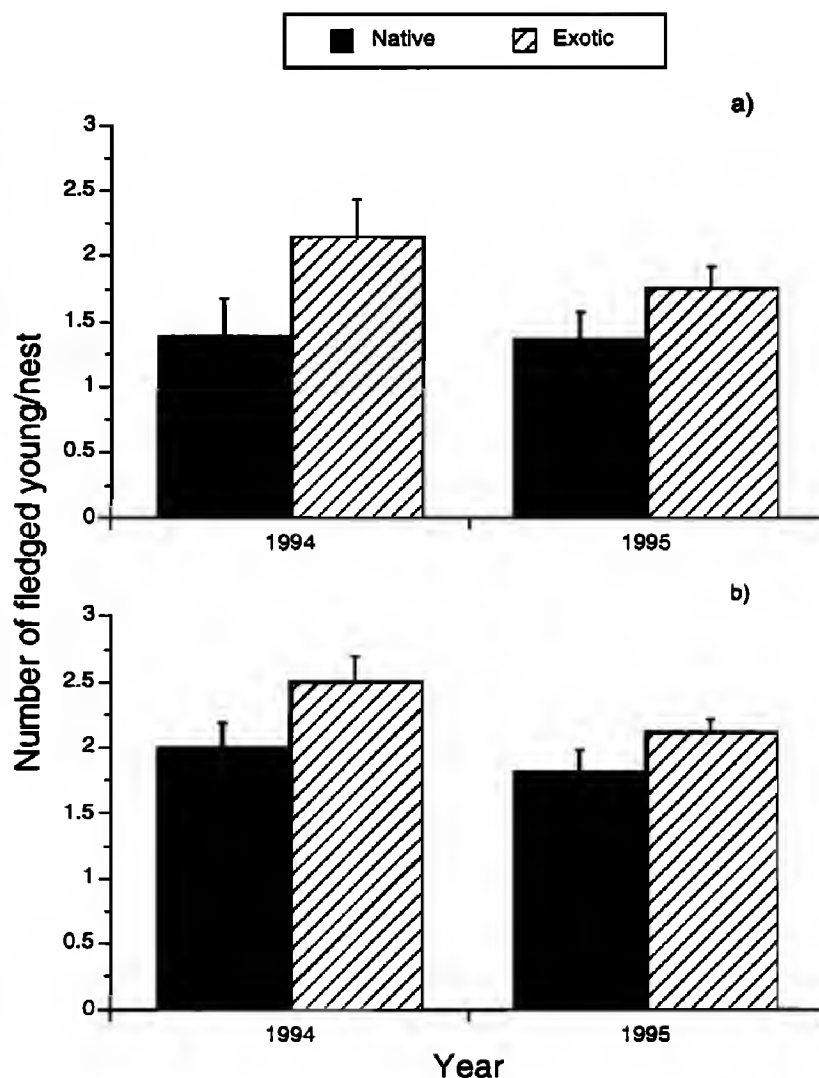


Figure 2. Mean number of fledged young per nest (a) and per successful nest (b) in native and exotic trees used for nesting by Red-shouldered Hawks.

nests in native trees in 1994 were attended by a pair that included a subadult, and the mean number of fledged young per nest in native trees was significantly lower for those pairs containing a subadult than for pairs with two adults in 1994 ( $U = 38.5$ ,  $P < 0.01$ ). In 1995, three of 20 nests in natives (15.0%) and three of 38 nests in exotic trees (7.9%) had a subadult attending. Although two of the five unsuccessful native-tree nests in 1995 were attended by a subadult, differences in fledging success between pairs that did and did not include a subadult were not significant in that year. Nest success was also low for subadults that nested in exotic trees; the single pair with a subadult that nested in a fan palm in 1994 was unsuccessful, and two of the three pairs including a subadult that nested in eucalyptus in 1995 failed to fledge any young.

**Relationship of Habitat Variables to Reproductive Success.** The habitat and nest-tree variables measured at each nest differed little between successful and unsuccessful nests (Table 3). Nest-tree height and nest-tree diameter were the only vari-

Table 3. Comparison of nest tree and habitat variables between successful and unsuccessful Red-shouldered Hawk nests in 1994 and 1995.

VARIABLE	1994 NESTS		1995 NESTS	
	SUCCESSFUL NESTS (N = 21)	UNSUCCESSFUL NESTS (N = 6)	SUCCESSFUL NESTS (N = 48)	UNSUCCESSFUL NESTS (N = 10)
DISTWAT	180.1 ± 86.7	14.0 ± 6.4	127.7 ± 40.7	43.1 ± 12.9
TREEHT	24.4 ± 1.2	18.3 ± 0.9**	23.8 ± 0.8	21.6 ± 1.5
TREEDBH	101.3 ± 5.5	76.5 ± 2.7*	97.6 ± 2.9	89.5 ± 5.2
NESTHT	17.3 ± 1.1	13.5 ± 0.9	15.9 ± 0.8	15.2 ± 1.3
ELEV	183.9 ± 27.4	179.7 ± 53.74	258.6 ± 22.6	186.4 ± 36.4
ARTIF200	0.43 ± 0.06	0.47 ± 0.15	0.41 ± 0.04	0.46 ± 0.09
ARTIF500	0.45 ± 0.06	0.49 ± 0.16	0.43 ± 0.04	0.49 ± 0.08
DISTBUIL	109.1 ± 26.8	75.0 ± 31.1	93.0 ± 18.3	108.0 ± 35.5
DISTPAVE	80.6 ± 25.0	59.5 ± 24.3	65.5 ± 14.1	70.3 ± 19.2

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

ables having significant effects on nest success (and then only in 1994), with successful nests being taller and having a greater diameter than unsuccessful nests. The simple linear regressions between these habitat variables and reproductive success indicated that the number of young fledging per nest increased with increasing nest-tree height in both years and with increasing tree diameter in 1995 ( $P < 0.05$  for these individual regressions), but neither nest success nor fledging success was related significantly to variables representing the degree of urbanization around the nests. In fact, many of the nests found in this study were in heavily urbanized areas, and some trees supporting successful nests were located as little as 2 m from a building and 1 m from the nearest road.

#### DISCUSSION

Studies of nesting Red-shouldered Hawks in eastern North America have found few nests in exotic trees (Bent 1937, Henny et al. 1973, Titus and Mosher 1981, Dijak et al. 1990), probably because they have been conducted primarily in heavily forested areas. Even in California, most studies of Red-shouldered Hawks have reported few nests in exotic trees, owing in some degree to the rural or natural study areas used (Dixon 1928, Wiley 1975). However, 37.7% of the nests found in a study in southern California, which included some urban and suburban areas, were in exotic trees (Bloom and McCrary 1996). My results showed that Red-shouldered Hawks nesting in the heavily urbanized

south San Francisco Bay area commonly use exotic trees.

Although Red-shouldered Hawks in some parts of California nest in native oaks and pines well removed from riparian areas (Roberson 1993, P.H. Bloom pers. comm.), only one nest >100 m from a stream in this study was in a native tree. Large native oaks and California bays (*Umbellularia californica*) were present in some upland portions of the study area, but on the floor of the Santa Clara Valley, few native trees suitably large for nesting were present outside riparian areas. Therefore, the planting of tall, sturdy exotic trees in upland areas has provided a number of suitable nesting sites where few existed previously, greatly expanding the extent of suitable breeding habitat and increasing the number of territories within the study area.

Many pairs seemed to prefer eucalyptus even in riparian habitats where mature cottonwoods and sycamores were available. Numerous riparian nests were found in lone eucalyptus or small eucalyptus groves surrounded by mature cottonwoods and sycamores, and exotic tree species were used for nesting more often than was expected based on their availability. Hawks in the genus *Buteo* generally select nest trees in proportion to the availability of trees suitably large for nesting, rather than seeking out specific tree species (Dixon 1928, Bent 1937, Bednarz and Dinsmore 1982). The frequent selection of eucalyptus for nesting in this study likely reflects the taller, broader-limbed nature of many eucalyptus nest trees compared to the native trees available.

The higher nest and fledging success in exotic trees may reflect in part their greater resistance to wind damage. Damage to unstable nests by winds is a potentially important cause of nest failure or abandonment, and successful Red-shouldered Hawks tend to build their nests on large diameter branches that provide stability in high winds (Bednarz and Dinsmore 1982, Dijak et al. 1990). In my study, only one nest in an exotic tree was damaged significantly by wind in each year, whereas in native trees, four nests in 1994 and two in 1995 were heavily damaged by wind. Both nesting and fledging success tended to increase with tree height and diameter, probably due in part to the greater stability of large trees. In fan palms, nests were supported very well by a large number of thick petioles. In eucalyptus, and to a lesser extent in sycamores, nests were usually well supported by thick branches, providing a sturdy platform for nests; nesting success was similar in these two species. However, nests in cottonwoods, which had the lowest success, were usually supported by fewer, often more slender, branches than nests in other species.

It is possible that the evergreen nature of eucalyptus and fan palms provided some additional protection from predators and weather, as most nests were initiated before deciduous natives leafed out. Also, mammalian predators may have difficulty reaching nests in eucalyptus trees given these trees' height and slick, thick trunks, while the "skirts" of dead fan palm leaves may protect nests in palms from mammalian predators (P.H. Bloom pers. comm.).

The percentage of nests occupied by a subadult parent, which tend to have low nest success (Palmer 1988), was higher for native nests than for exotic nests in both years. Eight of 12 pairs with a subadult failed to fledge any young, and fledging success in native trees was significantly lower for pairs that included a subadult than for those including two adults in 1994. If eucalyptus trees confer some advantage to nesting hawks, then older, more experienced birds would be expected to prefer these trees, perhaps relegating younger birds to more marginal territories without tall eucalyptus.

The large number of Red-shouldered Hawk nests found in exotics and the concomitant high nest success seems to have bolstered Red-shouldered Hawk populations in California. The presence of these trees in riparian areas may have partially offset the loss of riparian woodland for this

species, and the addition of suitable nest trees in upland areas that previously lacked appropriate trees has likely augmented hawk populations.

Studies in some areas have found that this species is generally sensitive to disturbance, usually nesting far from human activity (Bednarz and Dinsmore 1981, Bosakowski et al. 1992). In my study, many nests were very close to homes, offices and busy roads, and neither the percent cover by developed areas around nests nor the proximity of nests to buildings and roads influenced nest success or fledging success. As reported by Bloom and McCrary (1996), urban-nesting Red-shouldered Hawks are well-adapted to urban environments, and many are quite tolerant of human activity.

Results of my study indicated that California populations of Red-shouldered Hawks have actually benefited from the planting of exotic trees in urban areas. However, these results should not be extrapolated to all Red-shouldered Hawk populations or to riparian-associated bird species in general. Populations of Red-shouldered Hawks in other parts of the species' range are still low or declining, and it appears that persistence of those populations is dependent upon the preservation of large tracts of native woodland (Bednarz and Dinsmore 1981, Peterson and Crocoll 1992). Also, the results of my study are not meant to encourage the planting of exotic vegetation. Exotic plants often lack the resources required by many native animal species (Anderson et al. 1977, Mills et al. 1989). Unlike the Red-shouldered Hawk, many riparian-associated bird species have not recovered from the effects of widespread riparian habitat degradation and do not nest frequently in exotic vegetation.

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## HABITAT USE BY RED-TAILED HAWKS WINTERING IN THE DELTA REGION OF ARKANSAS

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**ABSTRACT.**—We examined use and avoidance of specific habitat types by Red-tailed Hawks (*Buteo jamaicensis*) during the winter in Arkansas. We conducted biweekly road surveys to determine the relative number of hawks present throughout the winter season and to record which habitat types hawks used for hunting purposes. Available cover types were used significantly ( $P < 0.05$ ) out of proportion to their availability. A total of 55.6% of Red-tailed Hawks used rice fields, which made up 49.3% of the available habitat. Additionally, 12.1% of Red-tailed Hawks were in forest patches that comprised only 0.9% of our study area. Hawk numbers were less than expected in soybean fields with only 26.5% of red-tails observed in 39% of the available habitat. Likewise, 5.8% of Red-tailed Hawks were in wheat fields that made up 10.8% of the habitat available. Juveniles and adults were not observed to use the various cover types differently ( $\chi^2 = 2.221$ ,  $P = 0.528$ ). Numbers of Red-tailed Hawks over the winter season were significantly correlated with rodent numbers ( $r = 0.618$ ,  $P = 0.05$ ). Our results suggested that Red-tailed Hawks were both spatially and temporally affected by variations in rodent abundance during the winter in the Delta region of Arkansas.

**KEY WORDS:** Red-tailed Hawk; *Buteo jamaicensis*; habitat use; prey abundance; winter; Arkansas.

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Uso del habitat de *Buteo jamaicensis* que pasan el invierno en la region del Delta del Arkansas

**RESUMEN.**—Examinamos el uso y el rechazo de tipos de habitat por parte de *Buteo jamaicensis* durante el invierno en Arkansas. Llevamos a cabo conteos de carretera dos veces por semana para determinar el número relativo de gavilanes presentes a lo largo de la estacion invernal para registrar que tipos de habitat utilizaban para cazar. Los tipos de cobertura disponibles fueron utilizados significativamente ( $P < 0.05$ ) por fuera de las proporciones disponibles. Un total de 55.6% de los gavilanes utilizaron cultivos de arroz, equivalentes al 49.3% del habitat disponible. Adicionalmente, 12.1% de los gavilanes utilizaron parches de bosque los cuales representaban tan sólo el 0.9% del área de estudio. Los números de gavilanes fueron menores de lo esperado en cultivos de soya con tan solo 26.5% de los gavilanes observados en el 39% del habitat disponible. El 5.8% de los gavilanes fue encontrado en cultivos de trigo, los cuales representaban el 10.8% del habitat disponible. Los juveniles y adultos no utilizaron las coberturas indistintamente ( $\chi^2 = 2.221$ ,  $P = 0.528$ ). Los números de gavilanes durante la estación de invierno fueron significativamente correlacionados con los números de roedores ( $r = 0.618$ ,  $P = 0.05$ ). Nuestros resultados sugieren que los gavilanes cola roja, fueron ambos espacialmente y temporalmente afectados por las variaciones de abundancia de los roedores durante el invierno en la región del Delta de Arkansas.

[Traducción de César Márquez]

The Red-tailed Hawk (*Buteo jamaicensis*) is probably the most common raptor in North America occupying almost every region except the arctic circle (Preston and Beane 1993). It inhabits open areas interdigitated with trees throughout its range (Bednarz and Dinsmore 1982). Despite its abundance, relatively little is known about the wintering ecology and biology of the Red-tailed Hawk. A few

studies addressing the topic have been completed in recent years, including work by Preston (1990) in western Arkansas and Lish and Burge (1995) in western Oklahoma. However, neither of these studies addressed wintering habitat use by red-tails in agricultural areas.

Wintering hawks arrive in Arkansas in October from the northern prairie region in the northcentral states and Great Lakes region (James and Neal 1986). These hawks aggregate in the Delta region of Arkansas which, perhaps, supports the largest

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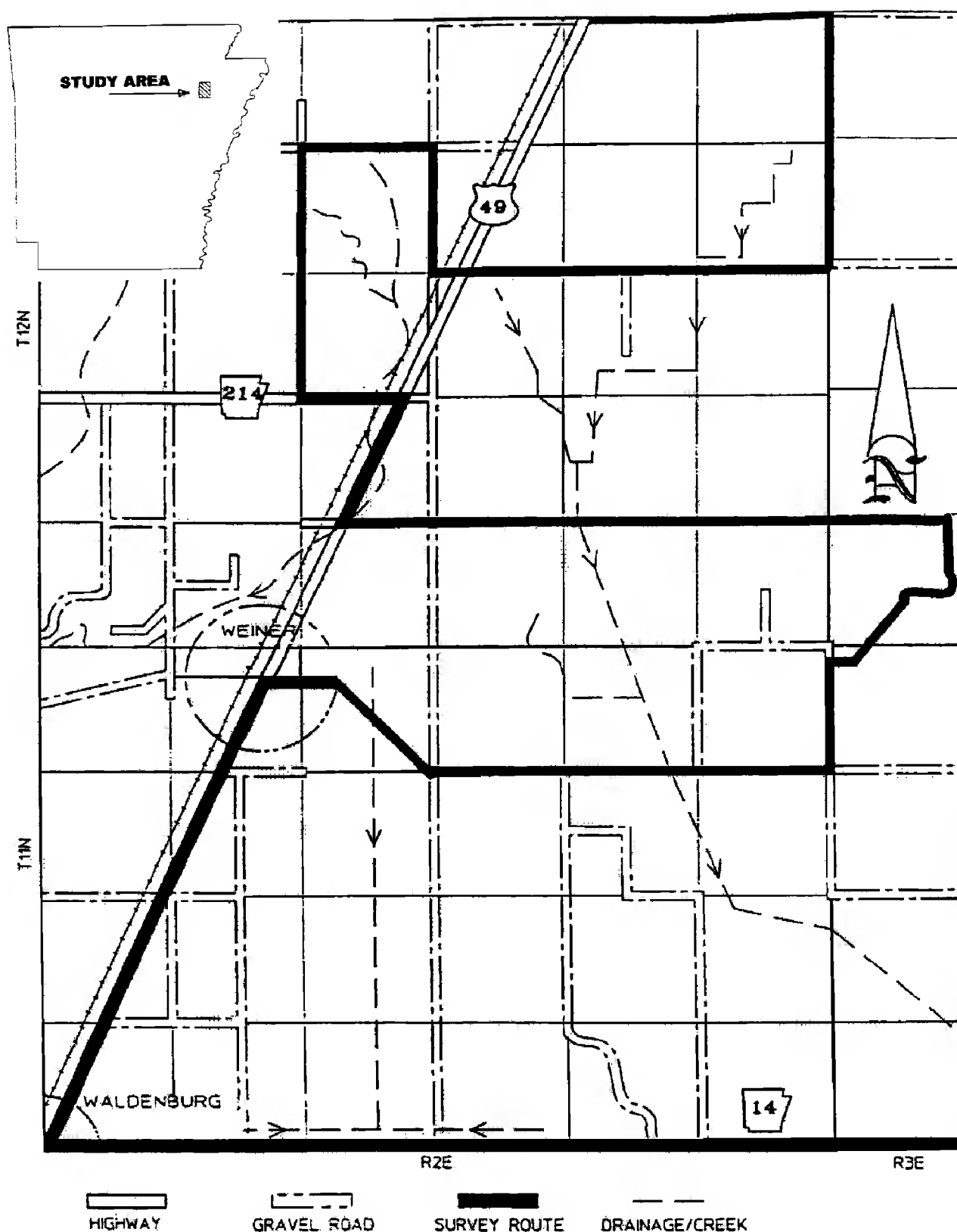


Figure 1. Map of the study area (101 km<sup>2</sup>) showing the raptor survey route (59 km). Each square represents 2.59 km<sup>2</sup>. The study area was located approximately 17 km south of Jonesboro, Arkansas, in northwestern Poinsett County (insert).

population of migratory Red-tailed Hawks in North America (Garner 1997). We initiated this study to increase our understanding of what factors contribute to the Red-tailed Hawk's winter abundance and their winter ecology in this region. Our primary objective was to determine whether Red-tailed Hawks use certain habitats or cover types more frequently and avoid others in the Delta region during the winter season. Our null hypothesis was that the hawks use all cover types in proportion

to their availability. The second objective of our research was to determine what factors may be responsible for certain preferences or avoidances of these habitat types.

#### STUDY AREA AND METHODS

The study area was located in northern Poinsett County, Arkansas, approximately 17 km south of Jonesboro, Arkansas (Fig. 1). It was rectangular in shape including 101.4 km<sup>2</sup> of agricultural land. Sections marking the four corners of the study area were: northwest—T12N, R2E,

S7, northeast—T12N, R3E, S7; southeast—T11N, R3E, S19; and southwest—T11N, R2E, S19. Weiner, Arkansas was just west of the center of the study area. The area was selected because large numbers of Red-tailed Hawks were observed in the area during years previous to our study (Hanebrink et al. 1978).

Historically, this area supported large stands of bottomland hardwood forests including dominant species such as white oak (*Quercus alba*), southern red oak (*Q. falcata*), hickory (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), sycamore (*Platanus occidentalis*) and baldcypress (*Taxodium distichum*). Understory species consisted of red maple (*Acer rubra*), elms (*Ulmus* spp.), green ash (*Fraxinus pennsylvanica*) (Preston 1989) and a variety of grasses and forbs. These communities were supported by periodic flooding of natural creeks and rivers in the area such as the Cache and L'Anguille River systems, as well as nearby Bayou DeView. All but a few of the historic bottomland communities were cleared for agriculture and timber production during the early 20th century (Wayne and Gatewood 1993). Today, this area, as well as most of the Arkansas Delta region, is primarily monoculture farmland producing rice, soybeans and wheat. These row crop fields are usually bordered by drainage ditches, small woodlots or occasionally fallow fields. Spillage of these crops (rice, soybeans and wheat) from trucks during transport provides food for rodents using grassy roadside habitats.

During the winter of 1995–96, cover types and woodlots were mapped by driving roadways in the study area and cumulative Red-tailed Hawk observations from all surveys were overlaid onto the cover map. All hawks recorded on these surveys were observed within 500 m of the roadway and the amount of available habitat was quantified for each cover type within this distance of the road. All hawk locations were categorized into one of the four cover types: rice fields, soybean fields, wheat fields and forested areas. Narrow ruderal roadside areas were not considered a cover type because all of the observations were made from roads. Therefore, all cover types where Red-tailed Hawks were observed were adjacent to roadside areas.

A cover map was also created using a geographic information system (GIS) data base. Roads, vegetation cover, human habitation areas and waterways were entered as data layers into a GIS. Data were digitized from Landsat 5 satellite imagery taken during May of 1992 and from topographic maps. The GIS image allowed an accurate measurement of cover types in the study area which did not change between 1992 and the time fieldwork was complete in 1996. A Bayesian classification program was used to delineate habitat types by statistically comparing reflectance values and combining them if no significant difference was detected. The changing crop types from year to year prevented accurate classification of row crop habitats based on the 1992 data. Therefore, all agricultural areas were lumped into one category, "row crops." The forested areas identified in the 1992 satellite image remained the same and were present in the study area during the 1995–96 winter season.

Cover types within the study area were as follows:

**Rice fields.** Rice was grown in the majority of the fields within the study area and were normally harvested by

October and the stubble was left standing throughout most of the winter until the planting season began in March. Many of these fields were intentionally flooded in winter to attract waterfowl. Rice fields were typically divided by several dikes which corresponded to a 2.54 cm change in elevation. These small dikes were constructed so that a constant water level was maintained within each partition of the rice field. Fields varied in size, ranging from <50–246 ha and were sometimes bordered by any of the other cover types.

**Bean fields.** Soybeans were the second most common cover type in the study area. Beans were usually harvested by the end of September or early October. These fields were seldom left with stubble after harvest and some were plowed under for the planting of winter wheat. After harvest, these fields contained virtually no cover and wildlife were seldom observed in them.

**Wheat fields.** These were relatively few in number. Wheat plants usually were not visible until December, at which time seedlings developed and provided some cover for wildlife. Wheat fields matured in May and were harvested in June, well after the winter study period. However, the seed was transported and planted during the winter season and spillage may have influenced the number of rodents using roadways during this period.

**Forests/woodlots.** Forested areas were fragmented and limited throughout the study area. Woodlots ranged in size from 0.5–80 ha and varied in age throughout the study area. These woodlots were composed primarily of hardwood species such as red oak, white oak, sweetgum, sycamore and hickory, as well as a variety of understory species. Woodlots typically followed drainage areas such as creeks and run-off ditches. Some smaller patches of forest, however, were in the middle of agricultural fields or along roadways. There were 21 separate woodlots present in the study area (excluding Bayou DeView Wildlife Management Area) that comprised a total area of 485 ha ( $\bar{x}$  = 23.1 ha).

**Fallow areas.** Fallow fields were the rarest cover type in the study area and were found within the city limits of Weiner, adjacent to grain elevators and between a railroad track and U.S. Highway 49. During the study period, crops were not planted in these areas or fields. Fallow fields supported native grass communities and early-successional plants including bluestem (*Andropogon* spp.), broomsedge (*Andropogon virginicus*), Indian grass (*Sorghastrum nutans*), goldenrods (*Solidago* spp.), prairie three-awn (*Aristida oligantha*) and sumacs (*Rhus* spp.).

**Water bodies.** A total of 17 water bodies was in the study area ranging in size from 3–61 ha ( $\bar{x}$  = 14.3 ha). Many of these ponds were constructed for fish farming or as irrigation reservoirs.

We established a systematic road survey (59 km) that ran throughout the study area (Fig. 1). During these surveys, all red-tails and other raptor species observed were tallied. Soaring hawks were also counted but were not included in the data analysis because no association with one habitat type could be determined. Two observers (one driver and one observer) were present during all surveys which were conducted between 0800–1200 H. Weather conditions varied among surveys; however, if there was steady rainfall or winds greater than 32 km/hr, we postponed surveys until the following morning.



Weather conditions were determined by reports supplied by the local airport via the National Weather Service. This same route was run approximately every 2 wk and the starting points of each survey were alternated in order to minimize a time-of-day bias. Subspecies or color morph (as described by Clark and Wheeler 1987), age (juvenile or adult) and location along the route were recorded for each hawk observed. Finally, we recorded the habitat type where each individual Red-tailed Hawk was observed.

The relative rodent abundance in each major habitat type was measured by trapping with Sherman live traps (Preston 1990). Traplines, consisting of 50 traps, each placed 10 m apart, were located in a rice field, woodland edge, roadside area, soybean field and wheat field. In the rice field, woodland edge habitat and roadside area, two replicate samples were collected on consecutive days (total sample = 100 trap-nights) twice during two field seasons (1994–95 and 1995–96). Data for only the 1995–96 field season are presented but results were consistent for both field seasons (Garner 1997). Rodent abundance was sampled (100 trap-nights) once in December–January and once in March within all habitat types and replicates. Soybean fields and wheat fields were sampled once during the 1994–95 field season but no rodents were trapped in either habitat type. Because of the low numbers of rodents using these areas, further trapping in these habitat types was stopped. Only the roadside and woodland edge sites were sampled for rodents in early March 1996 because the rice field habitat site was tilled under by late February.

Statistical analyses were conducted using Statistical Analysis System (SAS 1985) programs. Habitat availability and use were analyzed according to Neu et al. (1974). This analysis is performed using the distribution of hawks observed in certain cover types and comparing this to the number of hawks expected to use the cover types based on availability. Significance of use or avoidance was based on inclusion of the proportion of available habitat type within a confidence interval based on actual use of that habitat. Proportional use of specific habitat and cover types by juvenile and adult hawks was tested with a chi-square analysis. Pearson correlation analyses were also conducted to examine possible temporal relationships between observed hawks and rodent abundance. These correlations were based on rodent numbers sampled and the observed hawk numbers recorded on surveys conducted within 10 d of rodent sampling.

RESULTS

During the 1995–96 winter surveys, we recorded 275 Red-tailed Hawk sightings. We observed 153 (55.6%) hawks in rice fields and 73 hawks in soybean fields (26.5%). Rice fields were the most common cover type available (49.3% of the habitat surveyed) followed by soybean fields (39%; Table 1). We recorded 33 and 16 sightings in woodlots (forest edge) and wheat fields, respectively. Wheat fields comprised 10.8% of the cover types, and forests made up 0.9%. A slight preference was observed for rice fields (use = 55.6% vs. availability

Table 1. Habitat types and age class distribution of Red-tailed Hawks observed during raptor surveys in the winter (1995–96) in the Delta region of Arkansas.

HABITAT TYPE	AVAILABILITY (ha)	PROPORTION AVAILABLE TO HAWKS	EXPECTED NO. OF HAWKS	NO. OF OBSERVED HAWKS	PROPORTION OF USE	95% C.I. ON PROPORTION OF USE	% ADULT (N = 232)	% JUV (N = 43)
Rice	1590	0.493	135.6	153	0.556	0.474–0.638	87.0	13.0
Bean	1260	0.390	107.3	73	0.265*	0.192–0.338	79.5	20.5
Wheat	350	0.108	29.7	16	0.058*	0.019–0.097	81.2	18.8
Forest	30	0.009	2.4	33	0.121*	0.070–0.170	84.8	15.2
Total	3230	1.000	275	275	1.000			

\* Use of habitat was significantly different than available ( $\alpha = 0.05$ ).

Table 2. Relative abundance indices for rodents (rodents per 100 trap-nights) and species composition sampled in different habitats during the winter of 1995–96 and spring of 1996 in the Delta region of Arkansas.

HABITAT TYPE	DATE	RODENT INDEX	PERCENT COMPOSITION PER SAMPLE PERIOD				
			<i>Sigmodon hispidus</i>	<i>Oryzomys palustris</i>	<i>Microtus ochrogaster</i>	<i>Rattus norvegicus</i>	<i>Mus musculus</i>
Roadside	29–30 Dec	59/100	69.5	16.9	5.1	1.7	6.8
Rice field	6–7 Jan	13/100	7.7	38.5	15.4	0	38.5
Woodland edge	4–5 Jan	7/100	42.9	57.1	0	0	0
Mid-winter Means		26.3/100	40	37.5	6.8	0.6	15.1
Roadside	2–3 Mar	34/100	52.9	20.6	17.6	0	8.8
Woodland edge	4–5 Mar	1/100	0	100	0	0	0
Early Spring Means		17.5/100	26.5	60.3	8.8	0	4.4

= 49.3%), but this pattern was not significant ( $P > 0.05$ ). Soybean and wheat fields were avoided ( $P < 0.05$ ) by red-tails (Table 1). Hawks significantly favored woodlots ( $P < 0.05$ ), as these areas were overused (12%) compared to their availability (0.9%; Table 1). We observed mostly adults in all cover types (80–87%; Table 1). Juvenile numbers were slightly higher (20.5%) in soybean fields than in other habitats. The proportion of adults and juveniles observed among cover types, however, was not significantly different than expected ( $\chi^2 = 2.221$ ,  $df = 3$ ,  $P = 0.528$ ).

Roadsides were sampled first on 29–30 December 1995 resulting in a capture of 59 rodents during 100 trap-nights. This was the highest estimate of rodent relative abundance recorded during the early trapping period (December–January) (Table 2). Rice fields were sampled 6–7 January 1996, when we recorded an abundance index of 13 individuals per 100 trap-nights. The woodlot site registered a relatively low rodent relative abundance of 7 rodents/100 trap-nights. No rodents were captured during 100 trap-nights in bean and wheat fields sampled. Cotton rats (*Sigmodon hispidus*, 57%), rice rats (*Oryzomys palustris*, 24%) and house mice (*Mus musculus*, 11%) were the three most common species sampled during the 1995–96 mid-winter sampling period.

During the early spring sampling period, rodent abundance decreased in the two habitat types sampled with the woodland edge site showing the biggest decrease (7 to 1 rodent/100 trap-nights; Table 2). The roadside habitat produced a total of 34 individuals per 100 trap-nights; cotton rats were most abundant making up 52.9% of the sample.

Pearson correlation analysis of road census data with rodent sampling indices showed that Red-

tailed Hawk numbers and rodent numbers were positively correlated ( $r = 0.618$ ,  $N = 5$ ,  $P = 0.05$ ; Fig. 2), suggesting that Red-tailed Hawk use of habitats in the Delta may also have been correlated temporally with rodent abundance.

DISCUSSION

Based on 2 yr of winter survey data, we obtained an overall mean Red-tailed Hawk abundance index of 5.02 hawks observed per 10 km (winters of 1994–95 and 1995–96). Our findings surpass the highest densities previously reported by Lish and Burge (1995) in Oklahoma. They compared their findings of 3.78 hawks per 10 km to 23 other studies around the U.S. As far as we can determine, our data in Arkansas represent the highest winter density of Red-tailed Hawks ever reported based on extensive or repeat road surveys.

Hawk numbers were highest (55.6% of hawk observations) in rice fields along the road survey route; however, rice fields were also the most abundant cover type occupying 1590 ha (49.3%) of area sampled. The second most abundant field type along the route was soybeans (1260 ha). The second highest frequency of hawks (26.5%) was counted in bean fields but hawk numbers observed in these fields were less than expected when considering the availability of bean fields (39% of the study area). Hawks were observed using woodlots significantly more often (12.1%) than expected (0.9%) based on availability but used wheat fields less than expected.

Preston (1990) reported that a combination of rodent availability and vegetative structure influenced the distribution of foraging hawks during the winter in western Arkansas. He found that Red-tailed Hawks used corn stubble and “old fields”



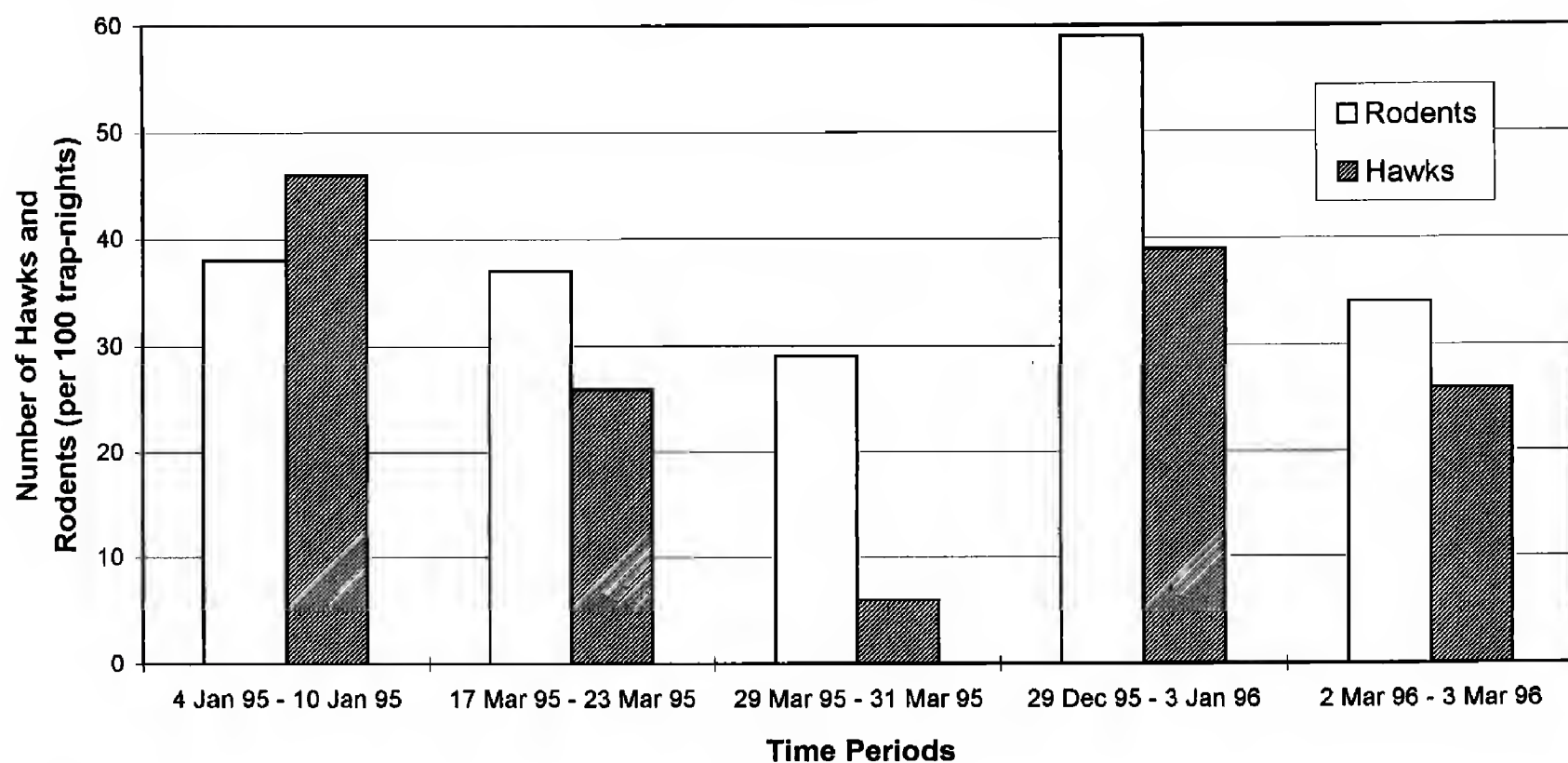


Figure 2. Total number of Red-tailed Hawks recorded during raptor surveys compared to rodent abundance indices in rice fields and roadsides sampled within the same time periods.

for foraging more than bare ground or tall corn. Similarly, Baker and Brooks (1981) found that Red-tailed and Rough-legged Hawk (*Buteo lagopus*) densities were relatively low in the habitat types with the highest meadow vole (*Microtus pennsylvanicus*) densities in Ontario. Based on this pattern, they suggested that vegetative structure of each habitat affected the vulnerability of the vole population. Habitat types with high densities of voles and high prey vulnerability (e.g., little cover) supported the highest densities of hawks. In our study, Red-tailed Hawks seemed to respond primarily to rodent abundance. This may have been attributed to the relatively similar vegetation structure found in both rice fields and roadside areas. Bean fields had little to no cover and supported few or no rodents. However, when cover was removed from rice fields by tilling, red-tails were observed to congregate in these fields and feed on fleeing rodents. This represents a case where the prey cover was substantially reduced, dramatically increasing vulnerability of rodents using those habitats. We observed at least 50 Red-tailed Hawks in one field while a tractor was discing rice stubble on 23 February 1995. Thus, in this aspect, our observations agree with Preston's (1990) that cover affects the prey vulnerability, and thus, availability of rodents. However, in the Delta region of Arkansas, winter cover normally does not vary among key habitats, including

rice fields until spring planting occurs and Red-tailed Hawks seem to respond to prey abundance in most circumstances.

Preston (1990) also suggested that perch availability influenced red-tail numbers using certain cover types. The abundance of utility poles along almost every roadway in our study area probably provided ample perch sites. In addition, woodlots provided essentially a continuous line of perch sites along the forest edge for red-tails that were likely foraging in adjacent cover types. The abundance of perch sites may explain the preference of Red-tailed Hawks for forests (woodlots) despite their lower rodent availability. The presence of hawks within or next to bean fields probably represented situations in which hawks were foraging in adjacent ruderal roadside habitats. Alternatively, some of these hawks may have been resting and not actually foraging. One notable difference between our study and Preston's (1990) study was the presence of roadside habitats. An abundance of roadways throughout our study area provided a substantial amount of ruderal roadside habitats, which may have supported higher numbers of rodents than the stubble fields sampled by Preston (1990).

The observations of overall higher rodent abundance along roadside habitats and that red-tails counted during surveys were within 500 m of road-

sides suggested that hawks were associated with roadside habitats. Rodent abundance along roadsides and rice fields was higher than in other available cover types and we suggest that this factor may explain the high hawk numbers observed adjacent to, or in, these habitats. Our sampling showed dramatic differences in rodent numbers between rodent-rich rice fields and roadsides and rodent-poor bean and wheat fields. Our casual observations suggested that these differences held true throughout our study area and throughout the winter; we frequently observed rodents during the day in grassy roadsides, but never saw a rodent in a bean or wheat field. However, we only sampled one example of each habitat with traps; most of these sites were sampled four times over two years with consistent results. These data supported the hypothesis that hawks more often occur near roadsides and rice fields because they support high densities of rodents, but this hypothesis requires further testing with replicate spatial sampling.

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## AN EVALUATION OF THE ANDEAN CONDOR POPULATION IN NORTHERN ECUADOR

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**ABSTRACT.**—We evaluated the population structure of Andean Condors (*Vultur gryphus*) in the Cotacachi-Cayapas and Cayambe-Coca Ecological Reserves, Ecuador. We conducted 1298 hr of fieldwork and made 496 condor observations. Age class and sex could be determined in 127 and 48 observations, respectively. The population consisted of 1:1 female to male ratio yet only 20% of our observations were of juveniles and subadults. The apparent skewed population structure suggested that the population may be declining.

**KEY WORDS:** *Andean Condor, Vultur gryphus; paramo; Ecuador; population structure; vulture.*

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Evaluación de la población del cóndor andino en el norte del Ecuador

**RESUMEN.**—Evaluamos la estructura de población del cóndor andino (*Vultur gryphus*) en las reservas ecológicas de Cotacachi-Cayapas y Cayambe-Coca, Ecuador. Llevamos a cabo un estudio de campo de 1298 horas e hicimos 496 observaciones de condor. Las clases por edad y sexo pudieron ser determinadas en 127 y 48 observaciones, respectivamente. La población consistió de 1:1 entre machos y hembras, tan sólo el 20% de las observaciones fueron juveniles y subadultos. La aparentemente sesgada estructura poblacional sugiere que la población puede estar declinando.

[Traducción de César Márquez]

The Andean Condor (*Vultur gryphus*) ranged historically from Venezuela to Tierra del Fuego (Murphy 1936). Its present range is greatly reduced (McGahan 1972, Lieberman et al. 1993) and the Andean Condor is now listed as Endangered over its entire range due to its precipitous decline (U.S. Fish and Wildlife Service 1986) and considered critically imperiled in Ecuador (Granizo et al. 1997). In Ecuador, condors inhabit the paramos above 3000 m (Josse and Anhalzar 1996). Carrion consisting of wild and domestic ungulates make up their primary diet (McGahan 1972). Given the patchy distribution of their food resource, group foraging behavior increases the probability of lo-

cating food over individual searching by lone birds (Wallace and Temple 1988a).

The paramo habitat is under heavy human pressures from agriculture, intensive livestock management and tourism (Caberle et al. 1989, Luteyn 1992). Numerous condors have been found dead in recent years but a systematic population study has not been conducted. This study was undertaken to evaluate the Andean Condor population in northern Ecuador.

### STUDY AREA AND METHODS

We conducted fieldwork from August 1996–March 1998 in the paramos above 3000 m of the Cotacachi-Cayapas Ecological Reserve (CCER; 0°25'N, 78°20'W) and the Cayambe-Coca Ecological Reserve (CAER; 0°08'N, 78°00'W) (Fig. 1). Additionally, we conducted fieldwork at Lake Mojanda, a proposed protected area (0°08'N, 78°17'W). All areas lie in northern Ecuador. The CCER is within the western cordillera of Imbabura Province and the CAER is in the eastern cordillera of Pichincha Province. Lake Mojanda lies between the cordilleras.

Paramo is an equatorial alpine grassland ecosystem dominated by bunchgrasses (*Festuca* spp.) and characterized by shrubs (*Polylepis incana*, *Brachyotum alpinum*, *B.*

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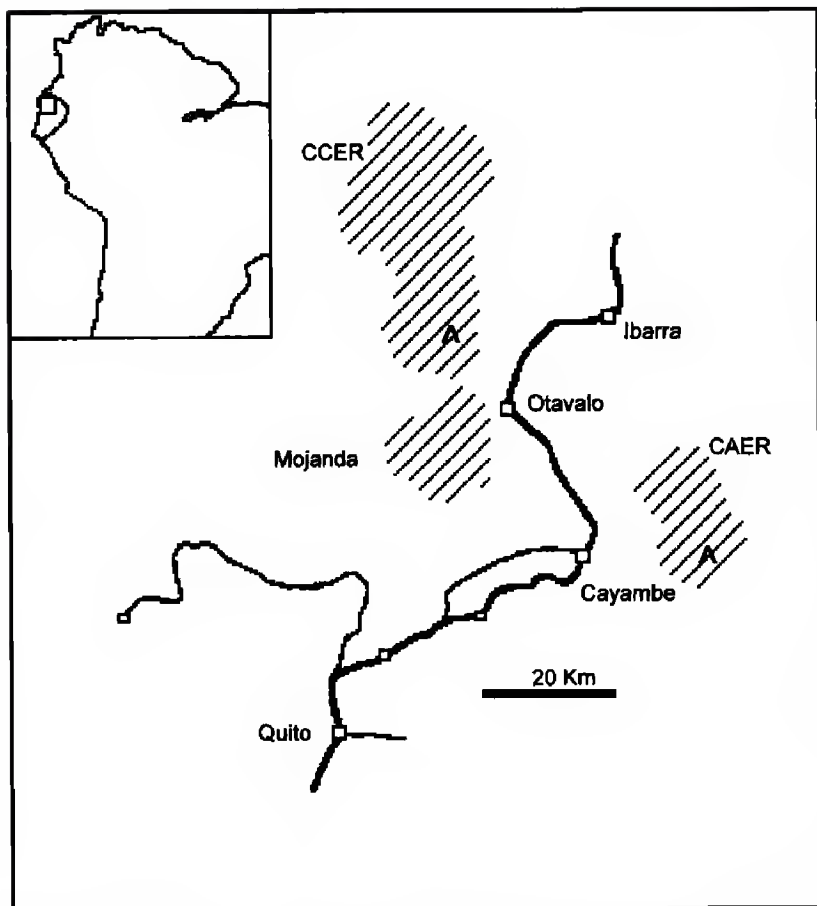


Figure 1. Approximate area (shaded) covered by condor surveys in 1996–98 in the Cotacachi-Cayapas Ecological Reserve (CCER), Cayambe-Coca Ecological Reserve (CAER) and Lake Mojanda area, Ecuador.

*ledifolium*, *Chuquiraga jussieu*), ground level plants (*Huperzia crassa*, *Valeriana rigida*, *Lupinus* sp.) and giant rosette-plants (*Puya* spp.) (Luteyn et al. 1992, Josse and Anhalzar 1996). The paramos cover approximately 25 000 ha (Josse and Anhalzar 1996), or roughly a little over 2% of Ecuador's landcover. Mean temperature is 8°C and total annual rainfall ranges from 900–2600 mm (Josse and Anhalzar 1996).

Surveys were conducted on week-long trips to the study areas. Day-long surveys were made from 19 ridgetops that were identified as condor viewing areas by park rangers and local residents who knew the study areas well. Ten of these ridgetops were located in CCER and known locally as: La Cienega, Pulumtura, El Campanario, Hacienda Chinchivi, Cerro Pilabo, Cerro Nagnaro, Cerro Quilili, Pantavi Grande, Pantavi Chico and Las Antenas. Eight sites were used in CAER: Rasochupa, Turupamba Chico, Turupamba Grande, Quebrada de Mirlos, Quebrada Chimborazo, Ancholas, La Dormida and El Verde. In addition, the area adjacent to Lake Mojanda was used.

Fieldwork was generally conducted during the day between dawn and dusk. Any surveys made while traveling through paramo by horse, foot, four-wheel-drive vehicles, or when stationary were counted toward hours in the field except during heavy rains when condors were less likely to be observed. All observations were made using 8× and 10× binoculars and 20–60× spotting scopes. Photographs of condors were taken with 280 mm and 500 mm lenses when possible from 13 August 1996–22 January 1997.

We distinguished individual condors based on feather

wear and molt patterns and identified sex when possible (Snyder and Johnson 1985). We noted condor behavior for evidence of breeding status (McGahan 1972, Palmer 1988). Condors were grouped into adult ( $\geq 8$  yr old) and immature ( $< 8$  yr old) age classes based on plumage characteristics described by McGahan (1972). We assumed that different age groups and sexes had equal chances of being observed in the field.

## RESULTS

We spent 1298 hr in the field and made 496 condor observations from 19 ridgetops. Of these observations, 298 condor sightings were in the CCER, 186 in the CAER and 12 at Lake Mojanda. For each hour spent in the field, we were able to make 1.3 min of condor observations. We were able to determine the sex in 48 observations and estimate the condor's age in 127 observations. Our sample revealed a male to female ratio of 1:1. Adults comprised 80% of condors aged giving us a 4:1 ratio of adults to immatures. The maximum number of condors simultaneously in view was eight birds in the CCER. We were able to identify at least seven adult and four immature condors for all study sites based on a comparison of feather characteristics and molt patterns.

One nest was reported to us in May 1996 and was situated 100 m above an active tunnel construction site adjacent to the CAER (INEFAN 1997). A second pair of adult condors was seen copulating in September 1997 near Lake Cuicocha of the CCER. The pair was seen repeatedly in the area through March 1998 but no nest was located. We found no signs of additional breeding pairs.

## DISCUSSION

The results of our study suggested Andean Condors may be undergoing a population decline in northern Ecuador. Temple and Wallace (1989) determined in Peru that Andean Condors  $> 6$  yr old had a 94% survival rate. Independent juvenile condors between 1–6 yr old had a 90% survival rate, whereas dependent juvenile condors  $< 1$  yr old had a 74% survival rate. Breeding once every 3 yr is required to maintain a stable population. Wallace and Temple (1988b) calculated that a 1:1 ratio of adult to juvenile indicated a population with pairs that were breeding about once every 2 yr. The adult male to female ratio (1:1) found in our study suggested that pairing should occur. However, the 4:1 ratio of adult to immature suggested that the population was declining because the adult cohort was not being replaced.

This skewed age structure in the population may be the result of high mortality. Five Andean Condors were reported dead in 1987 by Cayambe residents. INEFAN park rangers also reported six dead condors near the Antisana Ecological Reserve in 1988. Five more were found killed by unknown factors in CCER in the early 1990s. Causes of mortality were not reported. One condor, however, was reportedly killed by Compound 1080 in 1990 and a car collision was suspected as the cause of a mortality in 1996 (L. Martinez pers. comm.). Whereas we expected that immatures had a much higher mortality rate than adults (Wallace and Temple 1988b), we were unable to determine the degree that mortality factors affected the immature condor population in Ecuador. Given the low probability of finding or reporting dead condors, it was likely that these incidents represented a small fraction of the condors that presumably died since 1987.

The skewed age structure of this population might also have been due to the fact that these condors were not breeding at their full potential. We found no evidence of breeding pairs except for one nest and several copulation attempts by another pair of condors. Wallace and Temple (1988b) suggested that condors with food stress do not breed regularly. While food shortages were not implicated with the California Condor (*Gymnogyps californianus*) population decline (Johnson et al. 1983, Ogden 1985, Snyder and Snyder 1989), food availability shaped the condors' distribution patterns (Wilbur 1977). In Peru, Temple and Wallace (1983), found that 26% of released juvenile Andean Condors died of disease, starvation or unknown causes. The effect of food stress on the population in our study area was unknown.

Some factors associated with the California Condor decline have not yet been noted in Ecuador. Ogden (1985) and Wallace (1989), for example, reported that human disturbance around California Condor nests can be problematic. While evidence of human impact on Andean Condors is limited, we found that one young fledged successfully from a nest situated 100 m above a noisy construction site (INEFAN 1997). While this may have been an exceptional occurrence, it suggests that human disturbance to nesting condors may be tolerated.

High mortality rates or low reproductive rates will lead to a population that can only be sustained by immigration. Survival rates and reproductive rates of the condor population in Ecuador are not

known at present. We do know, however, that immigration occurs because at least two adult condors in the Cayambe-Coca Ecological Reserve were tagged with patagial markers and released in Colombia from captive reared stock (Lieberman et al. 1993).

It should be noted that our results may also be artifacts of a skewed or small sample. Although we assumed that both sexes and all age classes had equal chances of being observed in the field, this may not have been the case. Given its distinctive head shape, for example, adult males may be easier to identify than females, especially at a distance. We were able to positively identify the sex of only 10% of our observations leaving us a relatively small sample size. Behavioral differences between adult and immature condors may explain also some of the skewed age ratio. Daily activity patterns among California Condors, for example, were unpredictable (Wilbur 1980). Snyder and Johnson (1985) noted that movement patterns among California Condors were divided among breeding territories and foraging areas. Adults stayed close to their respective breeding areas while all age groups appeared to mix thoroughly in foraging areas (Snyder and Snyder 1989). If Andean Condors had similar behavior to California Condors and our observation sites were limited to breeding territories, then we would expect to see few juveniles. Although we attempted to address this issue by conducting studies at 19 sites, surveys at additional foraging areas may contribute additional results.

The current Andean Condor population of northern Ecuador is small and critically imperiled (Granizo et al. 1997). Further field studies are needed to determine the causes of condor mortality, the effect of food shortages on the population and to develop and implement a successful management plan. Ecuador's human population is expected to double in 28 yr (Caberle et al. 1989) and condor habitat will likely diminish greatly as people move higher into the paramos where condors live.

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### SUMMARY OF PHILIPPINE EAGLE REPRODUCTIVE SUCCESS, 1978–98

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**KEY WORDS:** *Philippine Eagle*, *Pithecophaga jefferyi*; *breeding success*; *population decline*; *forest fragmentation*.

The Philippine Eagle (*Pithecophaga jefferyi*) is one of the rarest eagles in the world. Its present status has always been regarded as critically endangered. Previous estimates of the Philippine Eagle population have been speculative (Alvarez 1970, Gonzales 1971, Rabor 1971). The most recent estimate suggests that the total population consists of between 300–500 individuals (Kennedy 1977, 1985). Philippine Eagles lay a single egg and have a 2-yr cycle between successive breedings when pairs breed successfully, but in cases when breeding attempts fail, adults breed the following year. Since work began in earnest on this species, a large amount of information on nesting successes and failures in Mindanao have been amassed. Here, we report this information based on records collected over the past 20 yr, and provide insights as to the key reason for the decline of the population.

#### METHODS

We compiled all existing information on the reproductive success of Philippine Eagles based on published (Kennedy 1985) and unpublished documents gathered by the Philippine Eagle Foundation (PEF) between 1978–98. We defined a successful breeding attempt as those with young eagles that survived until fledging. Nests were located by daily surveillance from vantage points, usually along mountain ridges and in areas where eagle presence was reported by local settlers. Observers stayed in these areas for about a week during the breeding season between August–December and from 0600–1500 H. Blinds were built in trees adjacent to nest trees, usually about 50–100 m away. Life history information was obtained and daily activities were recorded. A reward system for reporting occupied nests was initiated in 1981. From 1985 to the present time, the reward system was intensified and coupled with other on-site programs such as the development of community-based initiatives and conservation education activities. Reports of sightings were improved further by forging partnership arrangements with broadcasting stations in Mindanao Island.

#### RESULTS AND DISCUSSION

Prior to 1970, only one nesting pair of Philippine Eagles was located (Gonzales 1971). From 1978–83, several nesting pairs were intensively studied within the logging concession of the Paper Industries Corporation of the Philippines (PICOP) in Surigao del Sur and Davao Oriental provinces, and within the Mount Apo National Park (Kennedy 1981, 1985). This was a period when intensive logging operations occurred on Mindanao Island and many nesting areas were logged or altered by slash-and-burn farmers. Eight breeding attempts by 6 pairs failed (72.7%) out of a total of 11 attempts during this period (Fig. 1). One nestling was retrieved from a nest at Mount Apo National Park and is currently being kept at the Philippine Eagle Center in Davao City.

From 1984–88, the PEF and the Department of Environment and Natural Resources (DENR) monitored the breeding population. Of the eight pairs monitored, there were 11 breeding attempts. Four failed (36.4%) and four young (36.4% nesting success) were produced. This represented an 18.2% increase in fledging success compared to the previous period.

From 1989–93, 11 breeding attempts by nine pairs resulted in eight fledglings (72.7% nesting success) and, from 1994–98, 17 breeding attempts by 12 pairs resulted in a higher success rate (88.2%). The increase in breeding pairs was mainly due to an increased awareness by local people and increased observer effort and was not indicative of the recovery of the population. Other strategies such as the reward system and media-based information campaign have also been widely used by the PEF since the early 1990s to increase the information on the number of breeding pairs in the population. The increase in breeding pairs during the last decade may also have been due to increasing fragmentation of lowland dipterocarp rainforest that result in increased contact with settlers.

Breeding success based on eight pairs with >1 nesting attempt was estimated at  $0.38 \pm 0.14$  ( $\pm$ SD) young/pair/

Table 1. Summary of Philippine Eagle nesting records from 1978–98. All information taken from Philippine Eagle Foundation records unless otherwise stated.

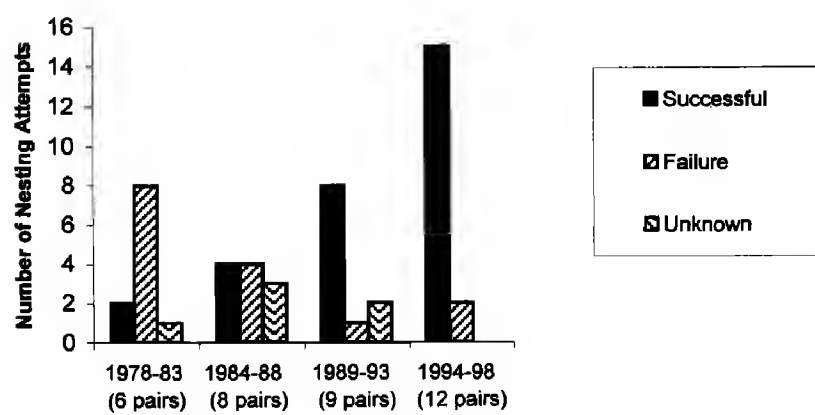
LOCATION <sup>a</sup>	YEAR(S) OBSERVED	NESTING STAGE OBSERVED	FLEDGING SUCCESS	COMMENTS
Mount Apo, Toril, Davao City <sup>b</sup>	1977, 78	Egg to nestling	Failed	Nestling died at 27 d
Amabel, Magpet, North Cotabato <sup>b</sup>	1978, 79	Nestling to post-fledging	Successful	
Kiandang, Magpet, North Cotabato <sup>b</sup>	1978, 79	Nestling to post-fledging	Successful	
PICOP, Surigao del Sur <sup>b</sup>	1978, 79	Incubation to nestling	Failed	Young died
Rd. 6P, PICOP, Surigao del Sur	1981	Courtship to nestling	Failed	Young disappeared after a storm
Rd. 78, PICOP, Surigao del Sur	1981, 82	Nestling	Failed	Young died
Mount Apo, Toril, Davao City	1983	Egg to nestling	Failed	Nestling died after retrieval due to apparent sickness
New Dumangas, Tiboli, South Cotabato	1983	Nestling	Failed	Young died after 4 mo
Amabel, Magpet, North Cotabato	1983	Egg	Failed	Egg abandoned, nest tree burned
Mount Apo, Toril, Davao City	1983, 84	Egg to post-fledging	Failed	
Rd. 6P, PICOP, Surigao del Sur	1983, 84	Egg to nestling	Unknown	Not revisited for verification
Laconon, Tiboli, South Cotabato	1985	Nestling	Unknown	Not revisited for verification
Upper Linan, Tupi, South Cotabato	1985, 86	Incubation to post-fledging	Successful	
Dalwangan, Malaybalay, Bukidnon	1986	Incubation to nestling	Failed	Eaglet retrieved by locals
Laligan, Valencia, Bukidnon	1986	Nestling	Failed	Eaglet retrieved by locals, later died
Salaysay, Marilog District, Davao City	1986	Post-fledging	Unknown	
Rd. 6P, PICOP, Surigao del Sur	1986	Incubation	Unknown	Not revisited for verification
Allah Valley watershed, Tiboli, South Cotabato	1986, 87	Incubation	Failed	Egg disappeared
Salaysay, Marilog District, Davao City	1987	Incubation	Failed	Egg added
Dalwangan, Malaybalay, Bukidnon	1987	Post-fledging	Successful	
Salaysay, Marilog District, Davao City	1988	Post-fledging	Successful	
Mount Apog-apog, Magpet, North Cotabato	1988	Post-fledging	Successful	
Dalwangan, Malaybalay, Bukidnon	1989, 90	Nestling to post-fledging	Successful	
Mount Apog-apog, Magpet, North Cotabato	1990	Nestling	Unknown	
Tambobong, Baguio District, Davao City	1990, 91	Incubation to post-fledging	Successful	
Guilang-guilang, Manolo Fortich, Bukidnon	1992	Nestling to post-fledging	Successful	
Freedom, Cabanglasan, Bukidnon	1992	Post-fledging	Successful	
Mamag, Ganatan, North Cotabato	1992	Nestling to post-fledging	Successful	
Mount Apo, Toril, Davao City	1992	Post-fledging	Successful	
Kibidtud, Tambobong, Davao City	1992	Nestling to post-fledging	Successful	

Table 1. Continued.

LOCATION <sup>a</sup>	YEAR(S) OBSERVED	NESTING STAGE OBSERVED	FLEDGING		COMMENTS
			SUCCESS	FAILED	
Salaysay, Marilog District, Davao City	1992	Nestling to post-fledging	Successful		
Dalwangan, Malaybalay, Bukidnon	1993	Nestling	Unknown		Nest not revisited
Kabalantian, Arakan Valley, North Cotabato	1993	Nestling	Failed		Young retrieved by locals after nest tree burned
Freedom, Cabanglasan, Bukidnon	1994	Post-fledging	Successful		
Dumalaguing, Impasug-ong, Bukidnon	1995	Post-fledging	Successful		
Guilang-guilang, Manolo Fortich, Bukidnon	1995	Post-fledging	Successful		
Mount Apo, Toril, Davao City	1995	Courtship to incubation	Failed		Egg addled
Dalwangan, Malaybalay, Bukidnon	1995	Incubation to post-fledging	Successful		
Mount Sinaka, Arakan Valley, North Cotabato	1995, 96	Incubation to post-fledging	Successful		
Salaysay, Marilog District, Davao City	1995, 96	Incubation to post-fledging	Successful		
San Fernando, Cabanglasan, Bukidnon	1995, 96	Incubation to nestling	Failed		Eaglet died
Lamlahak Lake, Sebu, South Cotabato	1996	Post-fledging	Successful		
Sobrecarey, Caraga, Davao Oriental	1996	Incubation to post-fledging	Successful		
Guilang-guilang, Manolo Fortich, Bukidnon	1997	Nestling to post-fledging	Successful		
Minlanga, La Paz, Agusan del Sur	1997	Post-fledging	Successful		
Mount Sinaka, Arakan Valley, North Cotabato	1997, 98	Egg to post-fledging	Successful		
Batian, Maitum, Sarangani Province	1998	Post-fledging	Successful		
Minlanga Range, La Paz, Agusan del Sur	1997, 98	Incubation to post-fledging	Successful		
Mount Apo, Toril, Davao City	1998	Nestling to post-fledging	Successful		
Salaysay, Marilog District, Davao City	1998	Incubation to post-fledging	Successful		

<sup>a</sup> Entry for location generally proceeds as a combination of the locality (barangay, mountain range or a road marker [e.g., Rd. 6]) and the municipality (or district), followed by the province (or city).  
<sup>b</sup> Kennedy (1985).





Relative number of successful vs. failed nesting attempts

Figure 1. Summary of the success and failure of Philippine Eagle breeding attempts based on 7-yr intervals.

yr and nesting success averaged 76.3% (Table 2). This was a conservative estimate since we did not take into account that eagles may have nested in following years after previous breeding attempts failed, instead of their typical 2-yr cycle. Many pairs had only one nesting record and these were excluded in calculating percent breeding success to minimize bias. One such pair at Rd. 6P PICOP, Surigao del Sur was documented to have bred three times during which one nesting attempt failed and the fate of the other two attempts were unknown. Some pairs, especially those within the Bukidnon province, had 100% breeding success rates while others like the pair at Mount Apo, Toril, Davao City had a 33.3% success rate and a productivity of 0.17 young/pair/yr. These differences may have been due to variation in food supply between the areas, differences in the ages of the breeding birds (Newton 1979), or simply an artifact of the small sample size. The overall success of Philippine Eagles averaged about 58.0% for 50 breeding attempts by 29 pairs from 1978–98. Based on the assumption that each breeding attempt had equal probability of success or failure, and that no regional differences existed among different pairs or subpopulations, we considered this productivity to be high and not indicative of a population suffering from breeding failures.

Precise assessment of the causes of breeding failure is difficult. Birds exposed to food shortages and disturbances during critical periods of the nesting cycle may abandon eggs or nests (Newton 1979). Our summary of causes of nesting failures (Table 1) was not complete because field methods varied over the years. Moreover, our results showed that many of the breeding pairs were disturbed by logging operations, slash-and-burn farming and by the observers themselves. Three of 15 failures (20.0%) were due to removal of young from nests or felling of nest trees with young. Most individuals currently kept at the Philippine Eagle Center in Malagos, Davao City were either confiscated or surrendered as juveniles. There were also three cases (23.5%) wherein eggs were added and/or abandoned, but the causes of nest abandonment were unknown.

The information we obtained may also have been based on the most conspicuous or accessible breeding pairs and, therefore, it may not be indicative of the true productivity of the population of Philippine Eagles. Some Philippine Eagle pairs may be more experienced breeders and may also be overrepresented in our sample which could account for the high reproductive success we recorded. Also, the high breeding success may also reflect the diminishing persecution of Philippine Eagles by the local people. Despite the limitations of the data we collected, we believe that it provides important baseline information to help focus future research and conservation efforts on the Philippine Eagle.

The current status of the Philippine Eagle as Critically Endangered is based mainly on the fact that this is a large-sized bird requiring a large territory and adapted to a tropical rainforest ecosystem that is fast disappearing in the Philippine archipelago. Theoretically, the assessment of raptor population stability involves integration of reproductive data with survival data for various age classes (Henny et al. 1970), but the lack of information on survival of Philippine Eagles after fledging limits the precise assessment of their population status. Although it is clear that the major threat to tropical birds of prey is forest destruction (Thiollay 1985, 1989, 1992), it was un-

Table 2. Breeding rates of Philippine Eagle pairs with more than one recorded nesting attempt.

BREEDING PAIR LOCATION	NO. BREEDING ATTEMPTS	% SUCCESS	BREEDING RATE (YOUNG/PAIR/YR)
Dalwangan, Malaybalay, Bukidnon	5	60	0.30
Minlanga Range, La Paz, Agusan del Sur	2	100	0.50
Freedom, Cabanglasan, Bukidnon	2	100	0.50
Guilang-guilang, Manolo Fortich, Bukidnon	3	100	0.50
Mount Apo, Toril, Davao City	6	33.3	0.17
Amabel, Magpet, North Cotabato	2	50	0.25
Mount Sinaka, Arakan Valley, North Cotabato	2	100	0.50
Salaysay, Marilog District, Davao City	6	66.7	0.33
Mean		76.3	0.38

clear whether the population decline of the Philippine Eagle is mainly due to reproductive failures or to increased mortality of juveniles, subadults and/or adults. A high rate of nesting failures could explain the population decline because Philippine Eagles lay a single egg and normally breed once every two years. Our data indicate that it is not nesting failures that are responsible for the population decline but that decreased survival of juveniles and subadults and their inability to disperse between forest islands to establish eventual breeding territories may be limiting the number of breeding pairs in this population. Past studies have suggested that the stability of breeding raptor populations is not related to prolonged good production of young but could be maintained by immigration or dispersal (Mebs 1964, Ratcliffe 1972, Newton 1979, Grier 1980). Nevertheless, forest fragmentation has untold effects on large tropical forest raptors such as the Philippine Eagle. Future research should focus on aspects of metapopulation dynamics such as survival and dispersal studies in a highly fragmented habitat, continued monitoring of reproductive performance of known breeding pairs in Mindanao and initiation of basic population ecology studies in other islands of the archipelago where Philippine Eagles are historically known.

RESUMEN.—El éxito reproductivo total del águila de las Filipinas (*Pithecophaga jefferyi*) promedio 58.0% de los intentos reproductivos por 29 parejas desde 1978–98. El éxito reproductivo con base en ocho parejas con mas de un intento reproductivo fue estimado en  $0.38 \pm 0.14$  ( $\pm$ SD) juvenil/pareja/año y el éxito reproductivo promedio 76.3%. Hubo 15 fracasos reproductivos, tres de los cuáles se debieron a la remoción de juveniles del nido o caídas del nido, y en tres casos los huevos fueron infértiles o abandonados. Nuestro análisis sugiere que los fracasos reproductivos no son un factor mayor en la declinación poblacional del águila de las Filipinas y apunta a un decrecimiento de la sobrevivencia de los juveniles y subadultos y su inhabilidad para dispersarse entre los fragmentos de bosque como la causa de la declinación numérica de esta especie.

[Traducción de César Márquez]

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## DIET OF AUTUMN MIGRATING NORTHERN SAW-WHET OWLS ON THE EASTERN SHORE OF VIRGINIA

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**KEY WORDS:** *Northern Saw-whet Owl*; *Aegolius acadicus*; diet; migration; pellet analysis; stomach-content analysis.

Although numerous studies have been conducted on the diet of Northern Saw-whet Owls (*Aegolius acadicus*), these accounts are almost exclusively limited to the spring breeding season (e.g., Cannings 1987, 1993, Marks and Doremus 1988) or the winter (e.g., Grove 1985, Swengel and Swengel 1992, Holt and Leroux 1996). It is well-known that many saw-whet owls make annual migratory movements to lower latitudes in the eastern and central U.S. (Mueller and Berger 1967, Holroyd and Woods 1975, Weir et al. 1980, Duffy and Kerlinger 1992, Brinker et al. 1997). However, little is known about saw-whet owl diets during autumn migration. The objectives of our study were to determine the diet of autumn migrating saw-whet owls, compare these results with data available from previous diet studies, and compare results obtained from pellet versus stomach-content analyses.

### STUDY AREA AND METHODS

Since 1994, migrating saw-whet owls have been trapped and banded each autumn just south of the city of Cape Charles (37°10'N, 75°50'W) on the eastern shore of Virginia (Whalen et al. 1997). Banding operations commenced during late October and ended in mid-December each year. Captured owls were kept in holding boxes before being banded and released. Although individuals were only kept in holding boxes for a short period of time, owls occasionally regurgitated pellets while in the boxes. From 1995–97, 1236 individual saw-whet owls were captured, from which a total of 53 pellets was obtained. These pellets were later dissected and prey remains were identified to the most precise taxonomic group possible. In addition to prey data collected from pellets, stomach contents were determined from 15 road-killed saw-whet owls found within 24 km of Cape Charles, mostly on U.S. Route 13. All road-kills were collected during autumn or early winter.

### RESULTS AND DISCUSSION

We identified 89 prey items from 53 saw-whet owl pellets (Table 1). Based on pellet analysis, lepidopterans

comprised 42.7% of all individual prey items taken by saw-whet owls. However, 78.9% of these insects were found in only two owl pellets containing 20 and 10 adult lepidopterans, respectively. Only six out of 53 pellets (11.3%) were found to contain insect remains and most of these also contained vertebrate prey. Thus, based on pellets alone, only a small fraction of saw-whet owls showed evidence of consuming insect prey.

Vertebrate prey remains were identified in 51 out of 53 pellets. Rodents and shrews comprised 96.1% of vertebrate prey. The most common prey species were white-footed mice (*Peromyscus leucopus*) and house mice (*Mus musculus*). Other prey identified to species included short-tailed shrews (*Blarina brevicauda*), a southern flying squirrel (*Glaucomys volans*), a silver-haired bat (*Lasionycteris noctivagans*) and a Vesper Sparrow (*Pooecetes gramineus*).

Out of 15 road-killed saw-whet owl stomachs analyzed, eight were empty and seven contained prey remains. In contrast to diet evidence from pellet analysis, five out of seven stomachs with prey remains contained insects. Ten individual prey items were identified from stomach contents, eight of which were insects and two of which were rodents (Table 1).

Although rodents probably comprise most of the prey biomass consumed by saw-whet owls migrating through the lower Delmarva Peninsula, the number of insect prey items is notable. More than 40% of prey items identified in pellets were lepidopterans. This stands in sharp contrast to findings from numerous breeding and winter diet studies (but see Hobson and Sealy 1991). Cannings (1993) summarized prey items taken by saw-whet owls in eastern North America, reporting that insects represented less than 1% of all prey items. More insects were identified from 53 pellets in our study than from several thousand pellets among all studies included in Cannings' account.

Our results from stomach analysis of road-killed owls provides even greater evidence that insects comprise an important part of the diet of migrating saw-whet owls. Since softer, more easily digested prey items such as invertebrates are often under represented in pellets, studies that rely exclusively on pellet analysis may poorly reflect actual diet composition. Although our sample size is small, 80% of prey items from stomach contents were

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Table 1. Prey remains of Northern Saw-whet Owls migrating through the eastern shore of Virginia during autumn 1995–97. Data are presented for prey items obtained from pellets ( $N = 53$ ) regurgitated by captured owls and from stomach contents of road-killed owls ( $N = 15$ ).

PREY TYPE	PELLET REMAINS		STOMACH CONTENTS	
	NO. PREY ITEMS <sup>a</sup>	PERCENT	NO. PREY ITEMS <sup>a</sup>	PERCENT
Mammals				
Short-tailed shrew ( <i>Blarina brevicauda</i> )	3	3.4	1	10.0
White-footed mouse ( <i>Peromyscus leucopus</i> )	11	12.4	0	0.0
House mouse ( <i>Mus musculus</i> )	7	7.9	1	10.0
Southern flying squirrel ( <i>Glaucomys volans</i> )	1	1.1	0	0.0
Unidentified rodent <sup>b</sup>	27	30.3	0	0.0
Silver-haired bat ( <i>Lasionycteris noctivagans</i> )	1	1.1	0	0.0
Birds				
Vesper Sparrow ( <i>Pooecetes gramineus</i> )	1	1.1	0	0.0
Insects				
Lepidoptera spp.	38	42.7	6	60.0
Homoptera spp.	0	0.0	1	10.0
Orthoptera spp.	0	0.0	1	10.0
Total	89 <sup>b</sup>		10	

<sup>a</sup> Some individual pellets and stomachs contained multiple prey items.  
<sup>b</sup> Most unidentified rodent remains consisted of post-cranial bones and bone fragments.

insects and one-third of road-killed owls contained insects in their stomachs. This finding was comparable to that of Hobson and Sealy (1991), who found substantial quantities of invertebrate prey remains in the stomachs of resident saw-whet owls on the Queen Charlotte Islands during the nonbreeding season. In their study, the majority of stomachs of road-killed owls contained marine invertebrate prey. Thus, small mammals probably represent the chief prey type for saw-whet owls throughout most of the year. However, invertebrate prey items may be taken opportunistically, especially during times when vertebrate prey abundance is low or unpredictable.

In recent years, the number of saw-whet owls trapped during migration in the Northeast has varied dramatically (Brinker et al. 1997, Whalen et al. 1997). The magnitude and dynamics of migratory movements by this species may be closely linked to the availability of prey relative to regional saw-whet owl population sizes. To the best of our knowledge, our study represents the first published account of the food habits of saw-whet owls during autumn migration. More information is needed on the diet composition of saw-whet owls, especially during summer and fall. In addition, information on small mammal and insect abundances along known saw-whet owl migration

routes could help to clarify the relationship between prey levels and the migratory behavior of saw-whet owls.

RESUMEN.—Los hábitos alimenticios de *Aegolius acadicus* durante su migración de otoño en la costa este de Virginia fueron documentados utilizando un análisis de egragópilas y contenidos estomacales. La mayoría de las presas (96.1%) encontradas en las egragópilas fueron roedores, especialmente *Peromyscus leucopus* y *Mus musculus*. Una larga proporción de insectos lepidópteros (42.7%) fueron también encontrados, pero en menor número de egragópilas. Otros tipos de presas en las egragópilas incluyeron *Blarina brevicauda*, *Glaucomys volans*, *Lasionycteris noctivagans* y *Pooecetes gramineus*. Los estómagos de 7 de 15 buhos muertos en las carreteras contenían comida. En contraste a los resultados de los análisis de egragópilas, 80 de los items de presas identificadas de los estómagos fueron insectos. Por lo tanto el análisis de egragópilas y contenidos estomacales pueden conducir hacia diferentes conclusiones acerca de la dieta de los buhos. En resumen estos resultados sugieren que los insectos juegan un papel importante en la dieta de la migración de *Aegolius acadicus* aunque los roedores representan la

mayoría de la biomasa de presas consumidas por esta especie.

[Traducción de César Márquez]

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## BREEDING BIOLOGY OF THE EURASIAN KESTREL IN THE STEPPES OF SOUTHWESTERN SPAIN

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**KEY WORDS:** *Eurasian Kestrel*; *Falco tinnunculus*; *laying date*; *clutch size*; *reproductive rates*; *steppe habitat*; *Spain*.

The Eurasian Kestrel (*Falco tinnunculus*) breeds in all countries of Europe. Its recent decline in the Palearctic has been linked to agricultural intensification (Tucker and Heath 1994), persecution, pesticides and climate change (Shrubb 1993). Several studies have shown large annual fluctuations in numbers of breeding pairs due to weather effects (Cramp and Simmons 1980, Kostrzewa and Kostrzewa 1990, Kostrzewa and Kostrzewa 1991) and rodent availability (Cave 1968, Cramp and Simmons 1980, Dijkstra et al. 1982, Bonin and Strenna 1986, Vilage 1990, Korpimäki and Wiehn 1998).

While population declines have been documented for the Palearctic, Tucker and Heath (1994) estimated that the breeding population of Eurasian Kestrels in Spain was relatively stable at 25 000 and 30 000 pairs. Aparicio (1997) postulated that the breeding population has been stable since the 1970s. Studies of the Eurasian Kestrel in Iberia have focused on the species' diet (Garzón 1974, Veiga 1982), nestling growth (Veiga 1985) and other ecological topics (Aparicio 1994a, 1994b, 1998). Data on the productivity of the breeding population in Spain are very scarce. The only published account to date is by Gil-Delgado et al. (1995), who reported on production in the Castellón province (eastern Spain).

Here, we report on the productivity of Eurasian Kestrels nesting in the steppe habitat of southern Iberia, Spain in 1989–90. We compare our results with data from other populations throughout the species' breeding range in the western Palearctic.

### STUDY AREA AND METHODS

We studied the breeding population of Eurasian Kestrels at La Serena, Extremadura, in southwestern Spain (38°50'N, 5°20'W). This area is characterized by dry pastures (64.2%) and cereal crops (28.4%; mainly wheat, barley and oats). There are also small areas of scrub (3.1%; mainly *Retama sphaerocarpa*) and areas with Holm-oaks (1.1%; *Quercus rotundifolia*) as well as fruit trees (mainly almond [*Prunus dulcis*]; Sánchez and Sánchez 1991). The study area has a mesomediterranean climate (Rivas-Martínez 1987). More information on the study area and its climate are reported by Avilés and Sánchez (1998).

In 1986, the Forestry Agency of Extremadura began a conservation project in the area that consisted of placing

900 wooden nest boxes in steppe habitat on electric power line stanchions (Sánchez and Sánchez 1991, Sánchez et al. 1996). In 1989 and 1990, 76 nest boxes were monitored weekly from the first stages of breeding. Visits were increased to 3–4-d intervals during the nestling period to more accurately determine factors influencing final breeding success. Laying date for each nest was determined by subtracting the incubation period of the species (28 d; Cramp and Simmons 1980) from the hatching date. Hatching date was determined by experienced observers, who took into account that all eggs hatch in 4 d (Cramp and Simmons 1980). We measured percent hatching success as the percentage of eggs within each clutch that hatched, percent nestling mortality as the percentage of young hatched that died in the nest, the number of fledglings per successful nest, breeding success as the number of fledglings per pair that laid at least one egg and percent egg productivity as the number of fledglings in each nest as a proportion of the total number of eggs laid in each nest.

Temperature and rainfall in the month previous to the onset of egg-laying were obtained from the meteorological station of Orellana, which is in the study area.

We tested for normality of the data with Kolmogorov-Smirnov tests. Only data on fledglings per successful nest and breeding success were normally distributed. For these two variables, analyses of variance and covariance were used for statistical analysis following Sokal and Rohlf (1979). A chi-square test was used to compare data on clutch size distribution to a Poisson distribution. Distribution of data on hatching success, percent nestling mortality and percent egg productivity were compared to a binomial distribution, also with a chi-square test. In no case was the null hypothesis rejected ( $P > 0.05$ ; data distribution did not differ from a Poisson or binomial distribution). Therefore, we ran a General Linear Model (GLM) for data with a Poisson distribution to study between-year and seasonal variation in clutch size, and a GLM for data with binomial distribution to study variation in hatching success, percent nestling mortality and percent egg productivity (Crawley 1993). We used the statistical software package "S-PLUS 4" to test GLMs with chi-square tests (MathSoft 1997). To avoid small sample sizes when clutch size was used as a factor, the extremely low clutch size of one egg was removed ( $N = 2$ ) from analyses. A Mann-Whitney test was used to test for between-year differences in laying date.

### RESULTS

Kestrels initiated egg laying on 10 April in 1990 and 23 April in 1989. The majority of pairs started laying dur-



Table 1. Comparisons of the reproductive performance of Eurasian Kestrels in southwestern Spain, 1989–90.

	1989 MEAN ± SD (N)	1990 MEAN ± SD (N)	STATISTIC P	BOTH YEARS MEAN ± SD (N)
Laying date	5 May ± 15.5 (26)	3 May ± 16.5 (49)	$U = 633.5$ 0.856 <sup>a</sup>	3 May ± 16.1 (75)
Clutch size	4.6 ± 1.9 (26)	3.9 ± 1.3 (49)	$\chi^2_{74} = 85.8$ 0.171 <sup>b</sup>	4.2 ± 1.3 (75)
Percent hatching success	84.4 ± 16.9 (24)	60.6 ± 37.5 (43)	$\chi^2_{289} = 375.2$ 0.0009 <sup>b</sup>	68.8 ± 33.4 (67)
Percent nestling mortality	0.0 ± 0.0 (22)	4.8 ± 15.0 (37)	$\chi^2_{206} = 139.3$ 0.491 <sup>b</sup>	2.9 ± 11.9 (59)
Fledglings per successful nest	4.0 ± 1.0 (22)	3.1 ± 1.4 (34)	$F_{1,55} = 8.2$ 0.006 <sup>c</sup>	3.4 ± 1.4 (56)
Breeding success	3.9 ± 1.3 (23)	2.4 ± 1.8 (43)	$F_{1,65} = 11.8$ 0.001 <sup>c</sup>	2.9 ± 1.8 (66)
Percent egg productivity	80.4 ± 24.3 (23)	57.4 ± 37.4 (43)	$\chi^2_{284} = 368.6$ 0.009 <sup>b</sup>	65.2 ± 34.8 (66)

<sup>a</sup> Mann-Whitney test.  
<sup>b</sup> General Linear Model.  
<sup>c</sup> Analyses of the Variance.

ing the first and second weeks of April. Mean clutch size was  $4.2 \pm 1.3$  eggs ( $\pm$ SD, range = 1–6 eggs,  $N = 75$ ; Tables 1 and 2). The most common clutches consisted of 4 (27.6%) and 5 eggs (33.5%; Table 2). A clear seasonal decline in clutch size was observed both in 1989 ( $b = -0.048$  eggs/day;  $\chi^2_{24} = 52.6$ ;  $P < 0.001$ ) and 1990 ( $b = -0.036$  eggs/day;  $\chi^2_{48} = 91.1$ ;  $P < 0.001$ ). We did not detect between-year differences in the seasonal trend in clutch size (interaction of year x laying date;  $\chi^2_{72} = 71.3$ ;  $P = 0.43$ ).

We detected no effects on reproductive performance when we evaluated the interactions among year, laying date and clutch size ( $\chi^2$  test and analysis of covariance;  $P > 0.05$  in all cases).

DISCUSSION

The onset of egg laying, percentage of eggs laid in April, clutch size and other reproductive rates observed in our study were within the range described for this species (Cave 1968, Shrubb 1970, Glutz 1971, Gordon and

Ridley 1979, Cramp and Simmons 1980, Bonin and Strenna 1986, Beukeboom et al. 1988, Hasenclever et al. 1989, Gil-Delgado et al. 1995). However, since our study was restricted only to pairs breeding in nest boxes, reproductive success may have been higher due to the potential for lower predation rates.

Some studies have shown large annual variation in laying dates, clutch sizes and reproductive rates in Eurasian Kestrels (Dijkstra et al. 1982, Beukeboom et al. 1988). Some of these have related variation in reproductive performance to weather conditions before egg laying (Kostrzewa and Kostrzewa 1990, Kostrzewa and Kostrzewa 1991). In our study, mean temperature in the month previous to the onset of egg laying did not vary between years and was 14°C in 1989 and 13.5°C in 1990 ( $P > 0.05$ ,  $N = 30$  in both years). However, in 1989, the month previous to the onset of reproduction was very rainy (84.1 mm in 1989 vs. 14.1 mm in 1990). Mean egg laying date and mean clutch size did not vary between years. Kestrel breeding performance, as measured by fledglings per

Table 2. Clutch sizes of Eurasian Kestrels in southwestern Spain, 1989–90.

YEAR	CLUTCH SIZE					
	1	2	3	4	5	6
1989	0	1	3	7	9	6
1990	2	8	5	14	18	3
Both years	2 (2.6%)	9 (11.9%)	8 (10.5%)	21 (27.6%)	27 (35.5%)	9 (11.9%)

successful nest and breeding success, was higher in 1989 when more rain fell. Grasshoppers (*Dociostaurus marrocanus*) are the primary prey of Eurasian Kestrels during the nesting season in Spain (Veiga 1985, J.M. Avilés and D. Parejo pers. obs.). Higher rainfall in the spring did result in an increase in grasshopper availability in our study area (Arias et al. 1993). Our study was not designed to evaluate potential relationships among rainfall, food supply and breeding performance so we could not be certain of the relationship, if any, among these factors.

We detected a clear seasonal decline in clutch size and fledglings per successful nest and breeding success in the La Serena population of Eurasian Kestrels. This trend has been found for other raptors (Newton and Marquiss 1984, Picozzi 1984, Hörnfeldt and Eklund 1990, Korpimäki and Hakkarainen 1991), including Palearctic populations of the Eurasian Kestrel (Cramp and Simmons 1980, Dijkstra et al. 1982, Meijer et al. 1988, Beukeboom et al. 1988).

The productivity of this population of Eurasian Kestrels was within the range described previously for this species in other areas. Although we found some evidence of improved reproductive output related to rainfall, more focused research is required to confirm our observations.

RESUMEN.—Se ha estudiado dos años la biología reproductora del cernícalo vulgar (*Falco tinnunculus*) nidificando en nidaes artificiales en zona esteparias del sudoeste en España. El inicio de la reproducción, la fecha media de puesta, el tamaño de puesta y el resto de tasas reproductoras estuvieron dentro del rango descrito para la especie en la región Paleártica. La especie mostró un descenso estacional significativo de su valor reproductivo. El número de pollos volados por nido exitoso y el éxito reproductor fueron mayores el año en que existieron mayores precipitaciones primaverales, sin embargo, la escasa serie temporal disponible no permite establecer una relación entre el nivel de precipitaciones y el éxito de la especie.

[Traducción de Autores]

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## BREEDING DENSITIES AND HABITAT ATTRIBUTES OF GOLDEN EAGLES IN SOUTHEASTERN SPAIN

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KEY WORDS: *Golden Eagle*, *Aquila chrysaetos*; *habitat*, *Mediterranean*.

Predictions on how animals respond to habitat changes are the primary aim of many conservation studies. Development of easy wildlife habitat models is an important tool for conservation and ecosystem management (González et al. 1992, Donazar et al. 1993). Progress has been made using Generalized Linear Models (GLMs) (Dobson 1983, McCullagh and Nelder 1989) to summarize the relationships between species distributions and environmental variables (Vincent and Haworth 1983, Nicholls 1989, Donazar et al. 1993).

It is known that patterns and processes in nature are sensitive to the scale at which they are viewed (Cody

1985, Wiens et al. 1987, Wiens 1989, Levin 1992, Lima and Zollner 1996). The scale at which systems are studied has a powerful influence on final conclusions and species-habitat relationships determined at one scale may not apply to others. Populations are influenced by the complex arrangement of habitat patches within landscapes and multiscaled studies seem to be the proper way to approach their study (Wiens 1989, Levin 1992).

The Golden Eagle (*Aquila chrysaetos*) is a raptor with a widespread distribution in the northern hemisphere. In North America, Steenhof et al. (1997) showed an important interaction between jackrabbit (*Lepus californicus*) abundance and weather on eagle reproduction and more recent work using radiotracking data (Marzluff et al. 1997) has noted the preference of Golden Eagles for some habitat types, particularly shrub and open lands. In



Europe, different qualitative descriptions around nest sites have been published (Tjernberg 1983, Watson 1997), and McGrady et al. (1997) constructed a model that delineated the area over which eagle pairs range and habitats of particular importance. More general approaches should be used as comparative parameters to consider entire populations and to reduce individual variability (White and Garrot 1990, Aebischer et al. 1993).

The purpose of this paper is to make a mathematical description of Golden Eagle breeding sites in southeastern Spain, where one of the highest densities of this species has been reported (Sánchez-Zapata et al. 1995). We propose a two-scale approach, considering at first responses around nest sites, and then a landscape-level analysis to evaluate the influence of the matrix on breeding territories.

#### STUDY AREA AND METHODS

The study area covered the Murcia region, a 11 317 km<sup>2</sup> area located in southeastern Spain with numerous mountains ranging from 0–2000 m elevation. The climate is Mediterranean arid and semiarid with a mean annual rainfall of 300 mm. Vegetation has a mosaic structure with cultivated lands (54%), grasslands and shrublands (28%), forest (15%) and open lands (3%) (Alcaraz et al. 1991).

All the territories known to be occupied by Golden Eagles at least once during the period 1985–97 were considered (Sánchez-Zapata et al. 1995). The location of breeding territories was incorporated into a Geographic Information System (IDRISI, Eastman 1992) using the UTM grid of 1 km<sup>2</sup> cells. For the first small-scale landscape approach the 1 km<sup>2</sup> cells were aggregated into 9 km<sup>2</sup> (3 × 3 km) cells, so the regional map of 11 317 km<sup>2</sup> cells was transformed into a map with 1381 cells of 9 km<sup>2</sup>. The large-scale landscape analysis was focused on 88 cells of 100 km<sup>2</sup> (10 × 10 km).

The same GIS was used to characterize the breeding sites using the following variables (Table 1): (1) SLOPE and LAND USE—slope (° from horizontal) was calculated from a Digitized Land Model 1:100 000 (Servicio Cartográfico Español) by comparing the altitude of each basic cell (200 × 200 m) with that of neighboring cells to the north, south, east and west. An average value for the different 200 × 200 m cells was calculated. Slope for larger cells (3 × 3 km and 10 × 10 km) was obtained as the mean value of 200 × 200 m subcells. These values ranged from 0–24.2 at the 9 km<sup>2</sup> scale and from 0.2–13.5 at the 100 km<sup>2</sup> scale. Different land-use classes were obtained from maps of the Ministerio de Agricultura (1:200 000) as proportions of cell area (9 km<sup>2</sup> and 100 km<sup>2</sup>) covered by each. New categories were formed by combining related land-use cover categories (e.g., lemon, orange and other fruit trees were combined to give a single arboreous intensive agriculture category). (2) EDGE—edge was measured as the length (km) of edges between different land uses using the digitalized land-use map and ATLAS GIS software. (3) STRUCTURE—number and size (ha) of the different patches of natural vegetation obtained from maps of the Dirección General de Producción Agraria (1:200 000).

Table 1. Variables used to characterize the breeding areas of Golden Eagles in southeastern Spain.

VARIABLES USED IN GENERAL LINEAR MODEL
LAND USE CATEGORIES
AINTA—% of cell covered by arboreous intensive agriculture, such as lemon and orange trees.
HINTA—% of cell covered by herbaceous intensive agriculture, such as vegetable crops.
AEXTA—% of cell covered by arboreous extensive agriculture, such as olive and almond trees.
HEXTA—% of cell covered by herbaceous extensive agriculture, such as cereal crops.
SHRUB—% of cell covered by shrubland.
FOREST—% of cell covered by forest, mainly <i>Pinus halepensis</i> .
SHF—% of cell covered by mixed shrubforest.
SLOPE—topographic irregularity index.
EDGES
EAEA—length (km) of edges between intensive and extensive agriculture.
FOIA—length (km) of edges between intensive agriculture and forest.
IASH—length (km) of edges between intensive agriculture and shrubland.
IASF—length (km) of edges between intensive agriculture and mixed shrubforest.
FOEA—length (km) of edges between forest and extensive agriculture.
EASH—length (km) of edges between extensive agriculture and shrubland.
EASF—length (km) of edges between extensive agriculture and mixed shrubforest.
FOSH—length (km) of edges between forest and shrubland.
FOSF—length (km) of edges between forest and mixed shrubforest.
SHSF—length (km) of edges between shrubland and mixed shrubforest.
STRUCTURE
PATCH—number of land-use patches per cell.
RICHNESS—number of different land-use patches per cell.
DIVERSITY—diversity (Shannon-Weiner) of land uses
NFOREST—number of forest patches per cell.
SFOREST—mean size (ha) of forest patches per cell.
NSHRUB—number of shrubland patches per cell.
SSHRUB—mean size (ha) of shrubland patches per cell.
NSHF—number of mixed shrub-forest patches per cell.
SSHF—mean size (ha) of mixed shrub-forest patches per cell.
NNAT—number of natural vegetation patches per cell.
SNAT—mean size (ha) of natural vegetation patches per cell.

Table 2. Response of Golden Eagles to the different habitat variables considered in southeastern Spain. % dev: deviance explained (ns—not significant, \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ . Responses: + s-shaped function, ++ bell-shaped function, – s-shaped function.

	SCALE			
	3 × 3		10 × 10	
	% DEV	RESPONSE	% DEV	RESPONSE
LAND USE				
AINTA	ns		ns	
HINTA	9.18*	–	11.37*	–
AEXTA	ns		ns	
HEXTA	7.65**	–	ns	
SHRUB	ns		ns	
FOREST	13.09***	+	22.81***	+
SHF	7.60*	++	21.88***	+
SLOPE	28.89**	++	42.12***	+
EDGES				
EAIA	6.76**	–	9.61**	–
FOIA	ns		ns	
IASH	ns		ns	
IASF	ns		ns	
FOEA	5.46*	+	14.45*	++
EASH	3.98**	–	ns	
EASF	ns		ns	
FOSH	2.88**	+	ns	
FOSF	4.95*	++	26.94***	+
SHSF	9.59***	+	ns	
STRUCTURE				
PATCH	2.58**	–	ns	
RICHNESS	3.11*	++	ns	
DIVERSITY	1.88*	++	7.33*	++
NFOREST	7.80***	++	ns	
SFOREST	11.34***	++	17.84*	++
NSHRUB	ns		ns	
SSHRUB	ns		ns	
NSHF	9.80**	++	8.31**	+
SSHF	5.24*	++	ns	
NNAT	1.96**	+	ns	
SNAT	11.60***	++	15.64*	++

Due to the effect of increasing sizes of cells, many of them included large areas of sea and adjacent regions that were not censused. Therefore, these cells were excluded from the data analysis making fewer breeding territories in the large-scale study (76 vs. 40 territories).

We used Generalized Linear Models (GLMs) to construct models of the breeding density of Golden Eagles (Dobson 1983, McCullagh and Nelder 1989, Nicholls 1989). For density response variables (number of breeding territories), the Poisson distribution was an adequate error function (Vincent and Haworth 1983) and the discrete Poisson function an appropriate link function ( $L = e^{(a+b_1x_1+\dots+b_kx_k)}$ ). This meant that the number of breeding

sites in an area was a discrete, s-shaped function when the linear predictor was the first order polynomial or a bell-shaped function for second order polynomials (Sánchez-Zapata and Calvo 1999).

For regression analysis, we used the program STATISTIX (Analytical Software 1992) following a forward stepwise analysis (Donazar et al. 1993). Each explanatory variable was tested for significance in turn. The variable contributing to the largest significant change in deviance from the null model was then selected and fit to the model. Once a variable was fit to the model, we tested if the addition of a second variable significantly improved the model. We chose a 5% level of significance to include a variable in a model.

Table 3. General Linear Model for Golden Eagle breeding density in southeastern Spain. % dev: deviance explained.

	COEFFICIENT	SE	P	% DEV
9 km <sup>2</sup> SCALE				
Constant	−6.55778	0.62282	0.0000	30.16
SLOPE	0.60749	0.12321	0.0000	
SLOPE <sup>2</sup>	−0.0167	0.00562	0.0000	
SHSF	2.034e <sup>−4</sup>	8.296e <sup>−5</sup>	0.0142	30.32
Constant	−6.64018	0.63324	0.0000	
SLOPE	0.60065	0.12638	0.0000	
SLOPE <sup>2</sup>	−0.01693	0.0058	0.0035	31.43
SHF	0.23580	0.10192	0.0207	
Constant	−6.86474	0.65345	0.0000	
SLOPE	0.54579	0.13264	0.0000	31.43
SLOPE <sup>2</sup>	−0.01445	0.00601	0.0162	
SSHF	8.415e <sup>−7</sup>	3.826e <sup>−7</sup>	0.0279	
SSHF <sup>2</sup>	−1.447e <sup>−13</sup>	7.055e <sup>−14</sup>	0.0402	
100 km <sup>2</sup> SCALE				
Constant	−0.75439	0.72879	0.0000	43.70
SLOPE	0.38313	0.05857	0.0000	
SHRUB	0.06663	0.03237	0.0396	

RESULTS AND DISCUSSION

SLOPE was the most important variable at both scales explaining a higher percentage at the 100 km<sup>2</sup> scale (28.89% and 42.12%, respectively). When scale changed, the response of eagles changed from quadratic to linear. *Pinus halepensis* forests (FOREST) was the second most important variable (13.09% and 22.81% for each scale) with a similar percentage of deviance explained by mixed shrubforest at the 10 × 10 km scale (21.88%). Intensive agriculture was negatively associated with eagles (HINTA 9.18 and 11.37%, respectively), while cereal crops were negatively correlated only at the smaller scale (HEXTA 7.65%) (Table 2).

Edges between land uses were also important at the larger scale, but explained low percentages of deviance at the 3 × 3 km scale. Edges between forest and mixed shrubforest (FOSF 26.94%) and edges between forest and extensive agriculture (FOEA 14.45%) were the most explanatory edge variable. Eagles responded negatively to edges between extensive and intensive agriculture at both scales (EAIA 6.76% and 9.61%, respectively). There was a negative relationship between eagle densities and edge between shrub and extensive agriculture only at the 9 km<sup>2</sup> scale (EASH 3.98%) (Table 2).

Percentages of deviance explained by landscape structure were generally low, except for natural vegetation and forest patch sizes (SNAT 11.60%, 15.64% and SFOREST 11.34%, 17.84% for each scale). At the 9 km<sup>2</sup> scale, the number of patches of natural vegetation and eagle densities seemed to be negatively related (PATCH 2.58%) (Table 2).

Because slope accounted for the higher percentages of

deviance, models were constructed entering SLOPE as the first variable. Only a small reduction in deviance was obtained by including other variables. At the larger scale, the model was more explanatory than at the 3 × 3 km scale (Table 3).

Because most Golden Eagles in Murcia nest on cliffs, slope was the most important variable in predicting its breeding densities. The linear response at the larger scale suggested that eagles preferred the bigger mountain systems of the region.

The primary factor influencing Golden Eagle breeding success is food availability (Steenhof et al. 1997). Eagles prey on medium-sized mammals such as jackrabbits (*Lepus* spp.) and rabbits (*Oryctolagus cuniculus*) (Steenhof et al. 1988, 1997, Watson 1997), which are very common in shrublands in Mediterranean areas (Moreno and Villafuerte 1995, Palomares and Delibes 1997). These open lands, where vegetation structure favors prey detection and hunting success (Tjernberg 1983, Marzluff et al. 1997, McGrady et al. 1997), were the second most important variable after slope in modeling breeding densities. Although forests seemed to be an important factor, this could have been a consequence of their distribution in the mountain systems of the area (Chaparro 1996).

Eagle densities were negatively correlated with irrigated crops, possibly because of the high number of people working in fields and their low prey populations. The increase in power lines associated with irrigated land could have also been an important negative factor for Golden Eagles, as electrocution is the main cause of mortality for many eagle species (González et al. 1990, Ferrer and Hiraldo 1992, Sánchez-Zapata et al. 1995).



RESUMEN.—Utilizando Generalized Linear Models (GLMs) examinamos la densidad reproductiva del Aguila real *Aquila chrysaetos* en relación con los usos del suelo, los bordes entre usos y la estructura del paisaje en el sureste de España. Las respuestas se compararon a dos escalas de paisaje. La pendiente fue la variable más importante para predecir la densidad reproductiva. Las manchas de vegetación natural se relacionaron positivamente con las águilas mientras que la agricultura intensiva se correlacionó de manera negativa. El matorral parece tener efectos positivos importantes, probablemente al incrementar la disponibilidad de alimento.

[Traducción de Autores]

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## TRAPPING ESTIMATES FOR SAKER AND PEREGRINE FALCONS USED FOR FALCONRY IN THE UNITED ARAB EMIRATES

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**KEY WORDS:** *trapping; Saker Falcon; Peregrine Falcon; Falco cherrug; Falco peregrinus; Middle East; falconry.*

Falconry in the Middle East depends on large numbers of wild-caught Saker (*Falco cherrug*) and Peregrine (*F. peregrinus*) Falcons (Allen 1980, Platt 1988, Remple 1988, Riddle and Remple 1994, Cade 1997). The larger female falcons are used primarily to hunt Houbara Bustard (*Chlamydotis undulata*), but some Saker Falcons are used for hunting Arabian hares (*Lepus capensis*). Smaller male Peregrine Falcons are more suited to catch Stone Curlews (*Burhinus oedinenus*). Falcons are trapped from as far as Eastern China to the Red Sea coast. Although information might be gathered from trappers or from markets, figures for the number of falcons being sold to the Middle East are difficult to collect and their reliability is questionable. Other species used in smaller numbers include Lanner Falcons (*F. biarmicus*), Laggar Falcons (*F. jugger*), Barbary Falcons (*F. p. peregrinoides*), Red-headed Falcons (*F. p. babylonicus*), Black Shaheens (*F. p. peregrinator*), Gyrfalcons (*F. rusticolus*) and captive-bred Gyrfalcon hybrids.

Since the early 1980s, professional veterinary care has been provided for these falcons with well-established clinics in Dubai, Abu Dhabi, Qatar, Bahrain and more recently in Saudi Arabia. At the Dubai Falcon Hospital (DFH), comprehensive computer records have been maintained since 1983. As many as 60 falcons are treated each day during the peak season. The majority of falcons admitted are from the United Arab Emirates with small numbers from other parts of the Middle East. An increase has been seen in the number of visits falconers make to the veterinary clinic. This is largely due to increased awareness amongst falconers and encouragement from the service being sponsored by H.H. Sheikh Hamdan bin Rashid Al Maktoum as a free service to the people. Many of the falcons are brought immediately upon purchase for routine checks and vaccinations and are therefore healthy on their first visit. The hospital is the most accurate source for information on falcon numbers and species within the region. In recent years, the majority of falcons seen at the Abu Dhabi Falcon Hospital have been hybrids. Hybrids are much less common in Saudi Arabia and the recent establishment of a falcon hospital in Riyadh should provide data, particularly on

the numbers of wild-caught Saker Falcons being sold to that region. This paper examines data collected on falcon numbers in the DFH from 1983–98. It is intended to estimate the minimum numbers of wild-caught falcons being used for falconry in the United Arab Emirates, mortality during the year, the proportion of captive-bred falcons being used and the species used.

### METHODS

Each falcon brought to the hospital was routinely allocated a sequential case number and accompanying veterinary record which included information on the species, sex, age, mass, relevant health problems and the owner's background. On its first visit, each falcon was implanted with a permanent microchip making it identifiable for subsequent visits. Any veterinary problems were treated and results of treatments, surgeries, microbiology, hematology and pathology were added to the computerized veterinary record.

A distinction was made between new falcons, total falcons and total visits. New falcons were those which had no microchip and were, therefore, assumed never to have been in the hospital before, or was implanted elsewhere but had never been to the hospital before. Total falcons were new falcons and falcons seen during the year which had been recorded at the DFH in previous years. Total visits were the sum of the number of visits made by each falcon during the year. No account is taken of length of stay in the hospital. The annual figures were calculated for the year beginning June 1, the peak falcon season being October–February.

Saker and Peregrine Falcons are the most popular species and they accounted for most of the falcons seen. For this reason, the data were analyzed separately and the data were for new falcons only each year. Very few captive-bred Saker or Peregrine Falcons are sold to the Middle East. Therefore, the figures were a good estimate for the number of falcons trapped.

### RESULTS

From 1983–84, the total number of falcons of all species brought to the hospital for treatment or routine checks was 73 (Fig. 1). This number increased to 2594 in 1997–98. During the 5-yr period from 1993–98, the numbers remained relatively constant despite the fact that very few falcons were not brought to the hospital.

Since 1993, a record was kept of the number of visits made by each falcon and hence a total number of visits for all falcons each year. The number of new falcons and the total number of falcons remained relatively constant (Fig. 2) averaging 1900 and 2400, respectively, each year.

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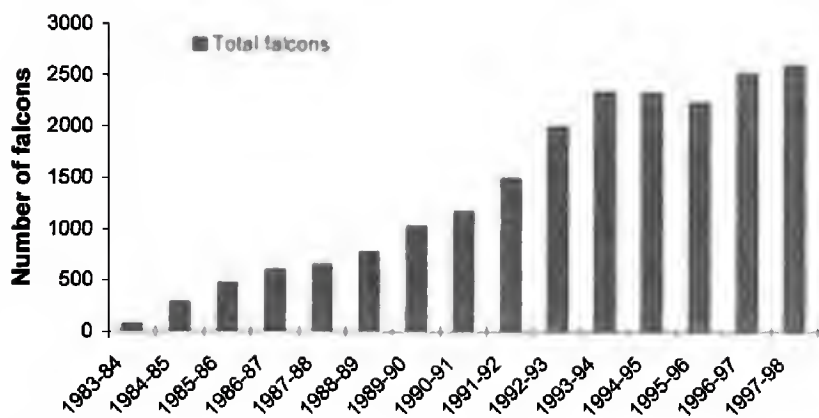


Figure 1. Total falcons admitted to the Dubai Falcon Hospital each year since 1983.

However, falcons were brought more frequently than in previous years with the total number of visits exceeding 5000 in 1995–96. No figure was available for 1997–98. Since 1993, approximately 25% of the falcons brought to the hospital in any one year had been to the hospital the previous year or before, an indication that most falcons were held during the summer months and used again the following hunting season. Of the other 75%, some were lost, released at the end of the season, died or were not brought to the hospital in subsequent years.

Both Saker and Peregrine Falcons were categorized by age and sex in 1993–98 (Table 1). The numbers were calculated as a percentage of new falcons (all species included) to indicate the changes within each species, sex, and age category. The total number of Saker and Peregrine Falcons remained fairly constant at about 1500 individuals, down from a maximum of 1953 falcons during the 1993–94 season. The total number of Peregrine Falcons increased by 12.5% over the 5-yr period, whereas Saker Falcon numbers decreased by 43%. The largest decrease was in juvenile female Saker Falcons.

There was a gradual decline in the percentage of Saker Falcons and an increase in the percentage of Peregrine Falcons. During 1993–94, Saker and Peregrine Falcons accounted for 94% of all new falcons seen. In 1997–98, they accounted for 74%. One reason for this decrease in Saker and Peregrine Falcons may have been the resurgence in popularity of captive-bred Gyrfalcons and Gyrfalcon hybrids. From a total of 58 hybrids seen in 1993–94, the number increased to 274 during 1997–98. However, in absolute numbers, Saker Falcons decreased from 1292 to 732 over the 5-yr period.

DISCUSSION

Within the United Arab Emirates, Saker Falcon numbers are decreasing whereas the numbers of captive-bred hybrids and Peregrine Falcons seems to be increasing. Historically, Peregrine Falcons were used more than Saker Falcons in the Gulf States. In the 1970s, there was a surge of captive-bred falcons into the Middle East, but their numbers subsequently decreased because falconers preferred wild-caught falcons. This attitude was largely

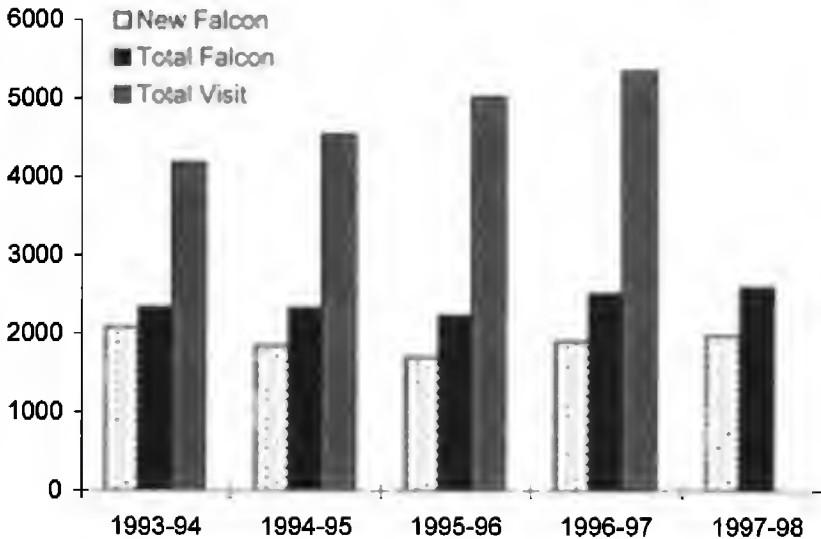


Figure 2. New falcons, total falcons and total falcon visits to the Dubai Falcon Hospital from 1993–98. No value was available for total visits in 1997–98.

due to falconers applying the same methods which they used to train wild falcons to training captive-bred falcons. Captive-bred falcons require different training methods and the Arabs did not get the best out of the falcons and were disappointed in them. There has recently been a resurgence in the number of captive-bred falcons used, partly because falconers have modified their training

Table 1. Numbers of new Saker and Peregrine Falcons admitted to the Dubai Falcon Hospital from 1993–98 calculated as a percentage of the total of new falcons admitted. All species included in parentheses.

	SAKER FALCON		PEREGRINE FALCON	
	MALE	FEMALE	MALE	FEMALE
1993-94				
Adult	26 (1.3)	225 (10.8)	19 (0.9)	81 (3.9)
Juvenile	112 (5.4)	929 (44.7)	189 (9.1)	372 (17.9)
Total	1292 (62.2)		661 (31.8)	
1994-95				
Adult	27 (1.4)	242 (13.1)	23 (1.3)	107 (5.8)
Juvenile	73 (4.0)	623 (33.8)	171 (9.2)	358 (19.4)
Total	965 (52.3)		659 (35.7)	
1995-96				
Adult	12 (0.7)	222 (13.1)	18 (1.1)	69 (4.1)
Juvenile	53 (3.1)	473 (27.8)	222 (13.1)	367 (21.6)
Total	760 (44.7)		676 (39.9)	
1996-97				
Adult	15 (0.8)	208 (10.9)	16 (0.8)	105 (5.5)
Juvenile	77 (4.0)	563 (29.5)	199 (10.4)	313 (16.4)
Total	863 (45.2)		633 (33.1)	
1997-98				
Adult	17 (0.8)	217 (11.0)	36 (1.8)	133 (6.7)
Juvenile	72 (3.6)	426 (21.5)	199 (10.1)	376 (19.0)
Total	732 (36.9)		744 (37.6)	



methods and because of the increasing interest in hybrids. Large, light-colored falcons have always been highly valued in Arabia. As such, pale colored Gyrfalcons and Saker Falcons were previously sought after. Survival of pure Gyrfalcons in the desert environment and Middle East climate requires special handling and fatalities are frequent. Large, pale, captive hybrids such as Gyrfalcon/Saker Falcon crosses combine the advantages of a desert-adapted falcon with a falcon of exceptional power and beauty.

Saker Falcon numbers, especially juvenile females, have fallen dramatically. During the 1997–98 season, 426 were admitted to the hospital compared to 929 in 1993. Data were collected at one hospital in Dubai, a rapidly developing country. In recent years, some sheikhs within Dubai have bought only large numbers of captive-bred hybrids. It is possible, therefore, that the market for Saker Falcons has concentrated on other regions of the Middle East. However, unless female Peregrine Falcons are preferred to female Saker Falcons, a similar decrease might be expected in Peregrine Falcon numbers. On the contrary, Peregrine Falcons have shown a recent increase.

Is the decrease in the number of Saker Falcons admitted to the hospital a real indication of fewer Sakers being trapped? If so, is this because of reduced demand or decreasing population numbers? Although juvenile numbers decreased, the number of adult Saker Falcons remained constant. Does this indicate that Sakers have experienced several consecutive poor breeding seasons? Almost every falcon is brought to the hospital at the start of the season for a routine check. Therefore, the difference in numbers between the species should not be attributed to some species being more susceptible to disease and therefore more often seen in the hospital.

The falcon species flown vary in different regions of the Middle East. For example in Taif, the plateau region in southern Hejaz, Saudi Arabia and on the Tihama plains adjacent to the Red Sea, Barbary Falcons are preferred. They are more suited to hunt Stone Curlews, Francolins (*Francolinus pondicerianus*) and Partridge (*Ammodendrix heyi*) found in this region. They are also cheaper to buy and more within the price range for people from this area than large falcons which sell for higher prices in the larger cities and which are used for Houbara Bustard and hares (Cade 1997). Laggar Falcons, Lanner Falcons and other small falcons are also trapped, but they have little financial value.

From the Dubai data, there is no evidence that the number of falcons being used for falconry is increasing. The number of falcons seen each year since 1993 remained relatively constant. Approximately 1500 Saker and Peregrine Falcons were brought to the DFH each year. In addition to these, falcons were trapped for sale in other parts of the U.A.E., Saudi Arabia, Kuwait, Bah-

rain and Qatar. Riddle and Remple (1994) estimated that there might be as many as 8600 Saker and Peregrine Falcons in captivity in the Middle East. It appears that there is considerable movement of falcons within the Middle East countries with falcons arriving in the Emirates and subsequently being moved to Saudi Arabia. If this is the case, then this figure would overestimate the actual number of falcons being used. Additional data from other falcon hospitals in the Middle East, especially Abu Dhabi and Riyadh, in conjunction with ongoing population studies should enable us to determine whether Saker and Peregrine Falcon populations can support this trapping pressure and, if not, what approach should be taken to regulate it.

RESUMEN.—El halcón sacre (*Falco cherrug*) y el peregrino (*Falco peregrinus*), son los halcones mas utilizados en la cetrería en el Medio Oriente. Los registros veterinarios en el hospital de halcones de Dubai proveen una base para estimar el número de halcones atrapados anualmente. Durante el período de 1993–98, el número de halcones peregrinos atendidos en el hospital se incrementó en un 12.5%, mientras que los halcones sacre disminuyeron en un 43%. Los híbridos de halcón gerifalte (*Falco rusticolus*) aumentaron en un 13.8% del total de halcones observados en la clínica. Las hembras juveniles de halcón sacre disminuyeron en un 54%.

[Traducción de César Márquez]

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## FIRST CONFIRMED BREEDING RECORDS AND OTHER INCIDENTAL SIGHTINGS OF NORTHERN HARRIERS IN LABRADOR

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**KEY WORDS:** *Northern Harrier*, *Circus cyaneus*; nest; breeding; distribution; Labrador.

The Northern Harrier (*Circus cyaneus*) is a globally distributed raptor of upland grasslands and fresh- and salt-water marshes (MacWhirter and Bildstein 1996). Populations in northeastern North America have declined precipitously over the past few decades (Kirk and Hyslop 1998). Through the early 1960s, Northern Harriers were recorded along the north shore of the Gulf of St. Lawrence near Natashquan (Todd 1963), but none were recorded as occurring in Labrador (Godfrey 1986). Recent range descriptions indicate that the northern extent of the breeding range falls south of the Labrador border (Macwhirter and Bildstein 1996) but, unlike most parts of its range, the Northern Harrier is extending its breeding range northeast into Labrador.

Herein, we describe the first known nest sites of Northern Harriers in Labrador and provide information on other recent sightings.

### METHODS

Most sightings were recorded during surveys conducted as part of the Environmental Mitigation Program for the Department of National Defence and for the Lower Churchill River Labrador Hydro Project. Other incidental observations were made opportunistically by the authors. Surveys have included the majority of Labrador south of 57°N and most of northeastern Québec, although no sightings were recorded in the latter region. Both nesting records were recorded during brief helicopter stops at the airport in Churchill Falls, Labrador.

### RESULTS

On 11 July 1998, a male Northern Harrier was seen flying over black spruce (*Picea mariana*) forest north of the airport runway at Churchill Falls, Labrador (53°34'N, 64°08'W). Shortly thereafter, a female Northern Harrier appeared and the male transferred prey to her in midair, and then flew away. The female flew low over an alder

(*Alnus* spp.) thicket and dropped to an unseen point on the ground.

We searched the area until we flushed the female. The nest was located on the ground in a band of alders 25 m wide on the north side of the runway. The alder thicket ranged in height from 1–3 m and was bordered by black spruce forest 30–50 m to the north. The nest was 15 m from the open edge of the runway and separated by a 1-m wide, water-filled ditch. The nest was a shallow bowl of grass (*Carex* spp.) approximately 30 cm in outside diameter with base material consisting of fallen alder leaves. The nest was on gravel with some mosses and grasses growing nearby. It contained one young <2-d old and two white eggs.

The nest site was revisited on 18 August 1998. Since our initial visit, the area had been clearcut of alders and all brush had been removed. There was no sign of the Northern Harriers or the nest. However, a low helicopter flight over the same area flushed a buff-colored juvenile Northern Harrier from the edge of the spruce forest less than 30 m from the site of the nest. The 38-d period between the approximate hatch date and this observation appeared to have been sufficient time for the young harrier to fledge from the nest.

On 10 May 1999, an adult male was flushed on the north side of the airfield and on 21 May a female was observed on the south side, an area with some remaining alders. On 25 May, we found a nest at the base of a group of alders near small spruce trees that contained one white egg. The base of the nest was constructed of dead alder stems <1.5 cm in diameter and was lined with dry grasses. The nest dimensions were approximately 45 cm outside diameter, 20 cm inside diameter and 8 cm deep. Ground cover within 3 m of the nest was comprised mainly of mosses (*Sphagnum* spp.), Labrador tea (*Ledum groenlandicum*) and sheep laurel (*Kalmia angustifolia*). The site was damp and interspersed with small pools of standing water from spring flooding. A nest check on 6 June showed the nest contained a clutch of 5 eggs. On 10 July, five young were observed and, on 29 July, three young



were banded and two had already fledged. The three banded young fledged on 30 July. These fledging dates were consistent with those detailed by Harrison (1984).

Most observations of Northern Harriers in Labrador were made in the coastal marsh areas of Lake Melville, the lower Churchill River valley and the south Labrador coast. The northernmost observation was an adult near Snegamook Lake (54°35'N, 61°20'W). Several sightings have been made of Northern Harriers in the Goose Bay area (53°20'N, 60°20'W) in each summer from 1996–99. Other sightings include a female carrying food at Ter- rington Basin on 26 July 1998, a juvenile flying near Lac Brulé (52°20'N, 63°50'W) on 18 August 1998 and a pair flying near the Churchill River at the outflow of the Elizabeth River (53°14'N, 63°18'N) on 22 May 1999.

In the last decade, the Northern Harrier has expanded its breeding range on insular Newfoundland and is now a fairly common widespread breeder, especially on the Great Northern Peninsula. Regional increases in observations may be correlated with coinciding peaks in microtine populations (Hamerstrom 1979, Hamerstrom et al. 1985, Simmons et al. 1986). The species is now fairly common on the Labrador side of the Strait of Belle Isle where it is presumably breeding. Shrubland heath and alder thickets are common vegetation types in insular Newfoundland and Labrador and may represent a significant amount of suitable breeding habitat for Northern Harriers. Nest-site locations in Labrador have similar habitat to that used by Northern Harriers in other parts of their range (Hamerstrom 1969, Simmons and Smith 1985). Little information is available on the distribution and breeding range of Northern Harriers in northeastern Canada, specifically Labrador. If estimates in other northern regions by Potts (1998) are accurate, a significant proportion of the northeastern North American population may be unaccounted for due to lack of survey effort. Examination of potential suitable habitat in Labrador may reveal additional breeding localities.

RESUMEN.—*Circus cyaneus* es un ave poco común en el sur y centro de Labrador sin ningún registro previo de anidación. Detallamos observaciones recientes y la primera anidación exitosa de *Circus cyaneus* en Labrador.

[Traducción de César Márquez]

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all those involved in the collection of information. Special thanks are extended to D. Lemon and L. Grattan of the Labrador Hydro Project for their collaboration and the use of their data. W. Price and R. Neville were observers on many of the flights. G. Baikie of CFL Co. searched for and found the nest site in 1999 and provided resighting information. G. Goodyear of Universal Helicopters Newfoundland Limited conducted the banding of the nestlings and was the pilot during many of the surveys from which our observations were made. Comments by A.J. Erskine, K.L. Bildstein and an anonymous reviewer improved the manuscript.

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## LETTERS

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### FIRST NORTH AMERICAN RECORD OF A MELANISTIC FEMALE NORTHERN HARRIER

Melanism, or dark coloration that results from the excessive deposition of melanin pigments (Sage 1962, *Brit. Birds* 55:201–225), occurs in a diverse array of birds (Sage 1962; Gross 1965, *Bird-Banding* 36:240–242). Melanism is especially common in birds of prey, many of which display a well-documented dark-morph plumage (Brown and Amadon 1968, *Eagles, hawks and falcons of the world*, Vols. 1 and 2, McGraw-Hill Book Company, New York, NY U.S.A.). In these polychromatic species, dark morphs do not appear to be any less successful than their light-morph counterparts. In addition, melanistic birds reproduce successfully with both light and dark conspecifics (Palmer 1988, *Handbook of North American birds*, Vol. 5, Part 2, Yale Univ. Press, New Haven, CT U.S.A.).

Interestingly, given their prevalence in a variety of raptor species (e.g., Rough-legged Hawk [*Buteo lagopus*], Ferruginous Hawk [*Buteo regalis*], Eleonora's Falcon [*Falco eleonora*]), melanistic individuals appear to be exceedingly rare in certain birds of prey. Despite the fact that melanism has been documented for several Palearctic harriers (Brown and Amadon 1968; Cramp and Simmons 1980, *Handbook of the birds of Europe, the Middle East and North Africa*, Vol. 2, Oxford Univ. Press, Oxford, U.K.; Clark 1987, *Brit. Birds* 80:61–72), including the Hen Harrier (*Circus cyaneus cyaneus*) (Watson 1977, *The Hen Harrier*, T. & A.D. Poyser, Berkhamsted, U.K.), only one record exists of a melanistic Northern Harrier (*Circus cyaneus hudsonius*), a male observed in California (Howell et al. 1992, *West. Birds* 23:79–80). Here, we report the first North American record of a melanistic female Northern Harrier.

At 1334 H MST on 12 November 1998, we observed a dark harrier coursing over a field 5 km northwest of Charlo, Lake County, Montana (47°27'30"N, 114°13'30"W). We observed the harrier for approximately 40 min. Observations were made in good light with 10 × 50 binoculars and a 20–60 zoom spotting scope at distances ranging from 100–400 m. Despite its dark coloration, the harrier was easily identifiable by its characteristic flight and shape, its underwing markings, facial disk and hunting behavior. The bird's most notable feature was the absence of the characteristic white uppertail coverts (i.e., rump patch). Its head, back, uppertail coverts, breast and belly appeared to be black. On the upper wing, the marginal coverts were a dark brown with a hint of rufous. The location of this rufous area matched that of the tawny coloration on the upper marginal coverts of typical-morph birds. The dorsal side of the remiges were brownish-black giving them a slightly lighter appearance than the body. Although the upperside of the tail was darker overall, it was very similar to that of a typical female harrier and consisted of 3–4 bold gray and black bands and uniformly dark central rectrices.

The melanistic harrier's underwing coverts were uniformly blackish-brown, whereas ventrally the remiges were light grayish-silver with fairly dark barring on the secondaries and primaries, including the outer primaries. The underside of the tail was similar to the dorsal side in that it consisted of bold gray and black bands. Finally, the bird had a yellow cere and irides, the latter confirming this bird's status as an adult. Typical adult female Northern Harriers show dark barring on the underside of the remiges, particularly on the outer primaries, whereas typical adult males exhibit inky-black wing tips on the underside and a light underwing with a bold subterminal band along the secondaries (Clark and Wheeler 1987, *A field guide to hawks*, Houghton Mifflin Company, New York, NY U.S.A.). The overall pattern, particularly the barring of the underwing, of the melanistic individual that we observed helped confirm that it was a female. Howell et al. (1992) also determined the age and sex of a melanistic male Northern Harrier by eye color, underwing pattern and size. The melanistic female interacted with a juvenile Northern Harrier that was noticeably smaller and believed to be a male. Several minutes after finding the melanistic harrier, it stooped twice on the juvenile, which turned and presented its talons each time and then left the area. A few minutes later we watched the melanistic harrier catch and consume what appeared to be a vole (*Microtus* spp.). In the following 5 min, it made two more capture attempts (both on small mammals), one of which was successful. Overall, during our brief observation period, the melanistic harrier appeared to be hunting successfully, free of harassment by other harriers.

Despite daily visits to the area where we first observed this melanistic harrier and continued surveys over the next six months, we were unable to locate it again.

Unlike albinism, melanism is a heterozygous dominant trait (Sage 1962). However, Clark (1998, *Wilson Bull.* 110: 289–290) suggested that in monochromatic species, the spread of melanism may be inhibited by the inability of melanistic individuals to acquire mates and produce offspring. Although the occurrence of melanism in both female

and male Northern Harriers has now been documented, whether such individuals do in fact attract mates and reproduce successfully remains unknown.—**Chad V. Olson, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812 U.S.A. and Sophie A.H. Osborn, Division of Biological Sciences, University of Montana, Missoula, MT 59812 U.S.A.**

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### OBSERVATIONS AT AN AYRES' HAWK-EAGLE NEST IN KIBALE NATIONAL PARK, UGANDA

The Ayres' Hawk-Eagle (*Hieraaetus ayresii*), an inhabitant of forested and wooded areas of sub-Saharan Africa, has long been considered inexplicably rare throughout its range (Brown et al. 1982, *Birds of Africa*, Vol. 1. Academic Press, London, U.K.). Its breeding behavior has been observed at no more than six nests in Kenya (Brown 1955, *Ibis* 97:38–64, 183–221; Brown 1966, *Ibis* 108:531–572; Dewhurst et al. 1988, *Gabari* 3:85–93) and Zimbabwe (Phillips 1978, *Honeyguide* 94:27–39; Steyn 1982, *Birds of prey of southern Africa*, Tanager Books, Dover, U.K.), and some aspects of its biology and ecology are still considered unknown (Virani and Watson 1998, *J. Raptor Res.* 32:28–39). Here, I present information on the nest site, breeding phenology, and behavior of a nesting pair of Ayres' Hawk-Eagles in western Uganda.

In August 1997, I located an Ayres' Hawk-Eagle nest in the unlogged K-30 forestry compartment of Kibale National Park (0°13'–0°41'N, 30°19'–30°32'E), an area of moist, evergreen forest in western Uganda. A complete description of habitat and climate are provided by Struhsaker (1997, *Ecology of an African rainforest*, Univ. Presses Florida, Gainesville, FL U.S.A.). I monitored the nest through November 1997, checking it at least twice every month. Using 10 × 40 binoculars, I observed the nest from the ground about 30 m upslope of the nest. I observed the nest for 35.5 hr during 7 d of the incubation period and 50.5 hr during 7 d of the nestling period. Adult gender was initially determined by size dimorphism, but once confirmed, the darker female was easily distinguished from the lighter male.

Located on an 18° slope with a WSW aspect, the nest tree was a live *Lovoa brownii*, 38 m tall and 98 cm diameter at breast height. The tree had no vines, few epiphytes, and the crown was completely isolated from the surrounding canopy. The stick nest was positioned at a height of 32 m, at a four-way fork of a major branch. Located near the base of the crown, the nest was plainly visible from the ground, but well-shaded from the sun. I estimated from the ground that the nest measured 1.25 m across and 0.75 m tall. When first observed on 21 August 1997, the female was already incubating. Based on the behavior of the adults, I estimated that one nestling hatched 31–33 d later, between 30 September–2 October 1997. The nestling was first observed approximately three weeks later, when its head was visible above the rim of the nest. Observations were discontinued on 24 November 1997, approximately 54 d after hatching, when the nestling was nearly fully feathered and it spent most of its time standing at the edge of the nest.

During the incubation period, the female spent most of her time at the nest, either incubating (88%) or perched nearby (5%). The female was out of sight for only 7% of this time, for periods ranging from 2–32 min. In contrast, the male never incubated, made only short visits to the nest (2–14 min) and nest tree (15–19 min), and was out of sight for 97% of this time. I observed no deliveries of prey or nesting material to the nest during incubation; possibly some prey exchanges occurred away from the nest, where the female fed before returning.

After the nestling hatched, the female remained the primary nest attendant spending 61% of the observation hours brooding or feeding the nestling. When not tending the nestling, the female was perched at or near the nest 16% of the time and out of sight of the observer for 23% of the time. The amount of time the female spent away from the nest increased as the nestling grew. As during the incubation period, the male was out of sight for most (98%) of the observation hours. The male made seven visits to the nest during the nestling period delivering nesting material twice and prey once. Possibly some prey exchanges during the nestling period also occurred at some distance from the nest. Most prey arrived at the nest apparently plucked of fur or feathers; the female spent little time handling prey prior to feeding the nestling. I checked for prey remains beneath the nest tree throughout the incubation and nestling periods, but found none. Except for an unidentified, pigeon-sized bird, I was unable to identify prey fed to the nestling.

These observations showed the breeding behavior of Ayres' Hawk-Eagle in the Kibale National Park was similar to

other regions of Africa. Although I was unable to document the complete duration of the nesting cycle, I estimated that it fell well within the 45 d incubation and 75 d nestling periods reported by Brown et al. (1982). Similar pairings of dark females with light males have been recorded at at least two nests in Kenya (Brown 1966, Dewhurst et al. 1988). There are no records of nests containing more than a single nestling and records of two-egg clutches from South Africa are considered suspect by most authors (Brown et al. 1982, Steyn 1982). Adult behavior at nests in Kenya was consistent with my observations; incubation and brooding were conducted primarily or exclusively by the female, while the male made brief visits to the nest to deliver prey and nesting material (Brown 1955, Dewhurst et al. 1988).

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### A CASE OF NEST PREDATION ON TURKEY VULTURES NESTING IN ARGENTINA

The Turkey Vulture (*Cathartes aura*) is widely distributed along the American continent (May, J.B. 1935. The Hawks of North America. National Association of Audubon Societies, New York, NY U.S.A.) but its breeding range in Argentina is not well-known. Only three records on Turkey Vulture nesting have been published up to now. Martín De La Peña (1992, Guía de las Aves Argentinas. Literature of Latin America [Eds.], Buenos Aires, Argentina) found two nests in northeastern Argentina and Jerome Jackson refers to another nest found on the Falkland Islands (1983, Nesting phenology, nest-site selection and reproductive success of Black and Turkey Vultures. Pages 245–270 in S. Wilbur and J. Jackson [Eds.], Vulture biology and management. Univ. California Press, Berkeley, CA U.S.A.). Turkey Vultures have a very diversified selection of nest sites, including hollow logs, prostrate trees and stumps, sides of steep cliffs, abandoned buildings or just on the ground (Coles, V. 1938, Studies in the life history of the Turkey Vulture *Cathartes aura septentrionalis* Wied. Ph.D. dissertation, Cornell Univ., Ithaca, NY U.S.A.).

We found a Turkey Vulture nest in Lihue Calel National Park, La Pampa Province, Argentina in 1998. Lihue Calel National Park is located in the central region of Argentina (38°00'S, 65°35'W) and contains bare rock hills (elevation 589 m) surrounded by flat semiarid desert (elevation 300 m). Vegetation in the area is a fine-grained mosaic of open patches and scrubs, including *Larrea cuneifolia*, *L. divaricata*, *L. nitida*, *Prosopis alpataco* and *Condalia microphylla*. Each year from September–February, large flocks of Turkey Vultures are commonly observed soaring in the park but no nests have been recorded.

We found the nest on 21 November and the female was incubating two eggs in the nest. The vulture flew away as we approached the site. The eggs were weighed and measured (68.7 × 49.05 mm, mass = 82 g; 69.05 × 48.65 mm, mass = 82 g). The nest was on the north side of a hill approximately 40-m high. The nest was near the top of the hill on the ground in a circular (8 m in diameter) patch of bushes (*Geoffroea decorticans*, *Larrea nitida* and *Lycium gilliesianum*). Height of the bushes averaged 2.3 m and they were surrounded by grass and rocks. Two rocks 70-cm high protected the nest on the east and south sides. The nest was not in a depression and there were only 5 or 6 small twigs and some feathers next to the eggs.

On 26 December, we revisited the nest and found two young that we weighed and measured (950 g, total length 345 mm, wingspan 753 mm, wing chord 147 mm and culmen 17.15 mm; 1030 g, total length 358 mm, wingspan 842 mm, wing chord 172 mm and culmen 19.15 mm). Their breasts and backs were covered with down but all sheaths of primaries and secondaries extended through the down layer and remiges emerged out from their sheaths about 2–4 cm. On 12 January 1999, the young were not found in the nest and the remains of one of their wings was about 6 m from the nest. No signs or footprints of predators were found at the nest site but the nest may have been depredated by a felid, fox or reptile.

We wish to thank National Parks Administration of Argentina, staff of the Lihue Calel National Park, and special thanks to José Antonio Sarasola, Daniel Muñoz, Rene Barquin, Agustin Lanusse and María Cristina Martín.—**José Hernán Sarasola, Ramón Alberto Sosa and Juan José Maceda, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Uruguay 151, (6300) Santa Rosa, La Pampa, Argentina.**



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### DECLINE OF THE EGYPTIAN VULTURE (*NEOPHRON PERCNOPTERUS*) IN THE CANARY ISLANDS

The Canary Islands lie off the northwest coast of Africa 100 km (Fuerteventura) north of the Tropic of Cancer. There are seven islands and six islets of volcanic origin with mountainous terrain. The climate is subtropical. Since the beginning of the 20th century the Canarian Black Oystercatcher (*Haematopus meadewaldoi*) and the Red Kite (*Milvus milvus*), as well as two endemic subspecies, *Phylloscopus collybita exsul* and *Saxicola dacotiae muielae* (Emmerson et al. 1994, Catálogo y bibliografía de la avifauna canaria, Cabildo de Tenerife, Santa Cruz de Tenerife, Canary Islands) have become extinct as breeding birds. Here, we report on the population trend of the Egyptian Vulture (*Neophron percnopterus*) in the Canaries since the beginning of this century.

Our methods included a literature survey of all published and unpublished works referring to the species. We also conducted a census of Fuerteventura and neighboring islets, the only area where there is still a breeding population, and collected information on the breeding success of this island's population in 1998.

In the Macaronesian region, the Egyptian Vulture is found only in the Canary Islands and Cape Verde. In both cases, it is sedentary and does not migrate to the nearby African continent. The species is also considered accidental in the Azores and Madeira (Le Grand 1983, *Archipelago* 4:49–58; Bannerman and Bannerman 1965, *Birds of the Atlantic Islands*, Vol. II, A history of the birds of Madeiri, the Desertas and the Porto Santo Islands, Oliver and Boyd, London, U.K.). It was relatively abundant in the past in all the Canary Islands, with the exception of La Palma. Since the 1950s, populations have been declining both in the Canary Islands and Cape Verde.

The first census of the population of Egyptian Vultures in the Canary Islands was conducted in 1987. It showed that 31–37 pairs inhabited the islands with 26–31 pairs concentrated in Fuerteventura (Delgado et al. 1993, *Bol. Mus. Munic. Funchal* 2:77–78). The census we conducted in 1998 located only 18 nesting pairs of Egyptian Vultures in Fuerteventura with the possibility of two additional pairs that also probably bred on the island. There were 1–2 pairs in Lanzarote and only one pair on the islet of Alegranza making the total breeding population in the Canary Islands at about 22 breeding pairs. This represented a 30% reduction in the breeding population in 10 yr.

Of the 18 pairs monitored in Fuerteventura, 10 did not breed successfully. Five of these failures occurred when nests were deserted prior to egg laying, three occurred because the eggs were infertile and two occurred when young were stolen from the nests. Only nine young fledged from eight successful breeding attempts for a productivity of only 0.50 young per breeding pair. In other studies carried out in different European regions, the productivity was twice as high averaging 1.00 ( $N = 42$ ) young per breeding pair in Provence (Bergier 1985, *World Working Group for Birds of Prey*, *Bull.* 2:77–78), 1.10 ( $N = 117$ ) in the French Pyrenees (Braillon 1979, *Le Percnoptere dans les Pyrennes francais*, La grande faune pyreneenne et des montagnes d'Europe, Universite de pau et F.I.E.P., Pau, France) and 0.81 ( $N = 117$ ) in Navarra (Donazar and Ceballos 1988, *Ardeola* 35:3–14).

The theft of eggs and young from nests as well as poisoning and direct disturbances from people near nesting sites are probably factors causing the low reproductive rate of this population. The increasing importance of tourism on the island has caused the gradual abandonment of the traditional economy based on livestock grazing and agriculture and the opening of new roads and the growth of urban areas. Many vultures also die each year because of collisions or electrocution from overhead cables. A study carried out by Lorenzo (1995, *Ecologia* 9:403–407) found six dead adult and juvenile Egyptian Vultures along 45.3 km of powerlines.

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## COMMENTARY

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### HOW BEARDED VULTURES (*GYPÆTUS BARBATUS*) ACQUIRE THEIR ORANGE COLORATION: A COMMENT ON XIROUCHAKIS (1998)

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Bearded Vultures (*Gypaetus barbatus*) are unique among raptors in that they have cosmetic coloration in their plumage. The typical bright orange coloration of adults is due to iron-oxide particles that coat the otherwise pure white feathers in the head, neck and ventral parts (Cramp and Simmons 1980, del Hoyo et al. 1994). The initial debate on the origin of the pigmentation of Bearded Vultures was settled long ago by conducting chemical and physical analyses of the feathers (Berthold 1967, Brown and Bruton 1991), but one fundamental question remained. Do Bearded Vultures actively stain their feathers by seeking sources of iron oxide, or does the plumage accidentally acquire its rufous color from the rocks where the birds roost or from the water in which they bathe? In other birds where cosmetic colors have been reported from soils, it is possible that the pigments are acquired passively (Kennard 1918). Among waterfowl, for instance, stained individuals are common in species that dig for their food among the iron-rich mud in shallow waters, while those species that are unstained usually forage in deeper waters or in dry fields.

Until recently, it was thought that the adventitious pigmentation of Bearded Vultures was passively acquired from stained rock ledges because no birds had ever been seen bathing in red soils or rust-colored springs. Brown and Bruton (1991) contradicted their own hypothesis of accidental coloring which should have no adaptive advantage and proposed a functional hypothesis, based on camouflage and feather protection against abrasion or mallophaga, to explain the coating of plumage with iron oxides. In a recent letter to this journal, Xirouchakis (1998) provided a detailed account on how a Bearded Vulture seemed to produce red dust for bathing by pecking on an eroded limestone rock (terra rosa), but again contradicted himself concluding that feather coloration is passively acquired.

We believe there is now enough evidence to support the hypothesis that Bearded Vultures stain their plumage

deliberately. Particularly imposing is the body of work conducted in Austria by Frey and Roth-Callies (1994). They offered damp soils of different colors and provenances to 33 caged birds of different ages, as well as 12 captive-raised individuals at a release site in the Alps. Except for one blind captive bird that remained pure white, all birds always preferred damp red soils containing iron oxides when they were offered with other mud types. All individuals showed an active coloration behavior consisting of a species-specific bathing display that led to the characteristic rufous coloration. Bathing in damp red soils was a much more elaborate behavior than regular bathing in clean water that is commonly observed in captivity (Frey and Roth-Callies 1994) and in the wild (Brown and Bruton 1991). Water bathing, on the other hand, seems to be a common behavior in most vulture species that often gather to wash and loaf (Mundy et al. 1992).

Baths in red damp soil by Bearded Vultures lasted for up to one hour. First, the birds crouched on the red mud, then spread the damp mud that was adhered in their undersides to their shoulders and upper backs with their beaks and talons. Finally, the head was swung repeatedly between the head and shoulders. This type of behavior has even been filmed for the documentary "The Lammergeier is back," directed by Michel Terrasse. Bathing in red soils seems to be an innate behavior, as young captive birds raised in isolation showed this behavior as soon as they were presented with damp red soils.

Recent observations in the wild, including Xirouchakis's, also demonstrate that the cosmetic coloration of Bearded Vultures is deliberate. An adult Bearded Vulture was observed bathing in a rust-colored spring in the French Pyrenees in 1995 (Caussimont et al. 1995), in what may be the first reported case of a Bearded Vulture coloring itself in the wild. A similar observation has been recorded at a Bearded Vulture breeding territory in the Spanish Pyrenees. In January 1998, one adult Bearded

Vulture was seen landing on the ground, near the bottom of a cliff. It walked toward the cliff bottom and went out of sight, but soon reappeared with its breast wet and dirty. It went there once more, and still moved to a second spot located a few meters away, coming out with its breast soaking wet. When these places were inspected, the first one had a rusty soil dampened by a slight trickle of water, and the second had a small ( $<1 \text{ m}^2$ ), transparent pool with iron oxides at the bottom. There were orange splashes in the surrounding snow and some feathers that were collected. We visited this place three more times in the following months (February, April and October) and found new feathers each time, indicating that Bearded Vultures had later returned to bathe. These observations suggest that color intensity, and thus the great individual variation observed in some populations, such as the one in Crete (Xirouchakis 1998), southern Africa (Brown and Bruton 1991) and the population that we are studying in the Spanish Pyrenees, is at least partly related to the frequency of baths and/or chromatic variations that are in different substrates such as in rust-colored springs. Suitable sources of iron oxides for plumage staining may be limiting for Bearded Vultures (Houston et al. 1993), and thus not all individuals in a population would have ready access to color sources, particularly if they are within the defended territories of conspecifics.

Despite many hours of systematic observations, including the tracking of radio-marked birds in southern Africa, the Alps and Pyrenees, the only reported observations of Bearded Vultures bathing to color their feathers are the ones that we mention. As suggested by Houston et al. (1993), coloration of feathers by bathing in wild Bearded Vultures is a very secretive behavior, quite different from the often communal and conspicuous bathing of other vulture species (Mundy et al. 1992). Nevertheless, it is a sophisticated behavior. The next question that needs to be explored is why do Bearded Vultures coat their plumage to such an extent all across their breeding range in Eurasia and Africa. Now that solid evidence of deliberate staining of the feathers in this species is accumulating, it is legitimate to look for an adaptive explanation.

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